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Explaining population size of the rare saproxylic beetle *Prionus coriarius* as a function of available dead wood resources

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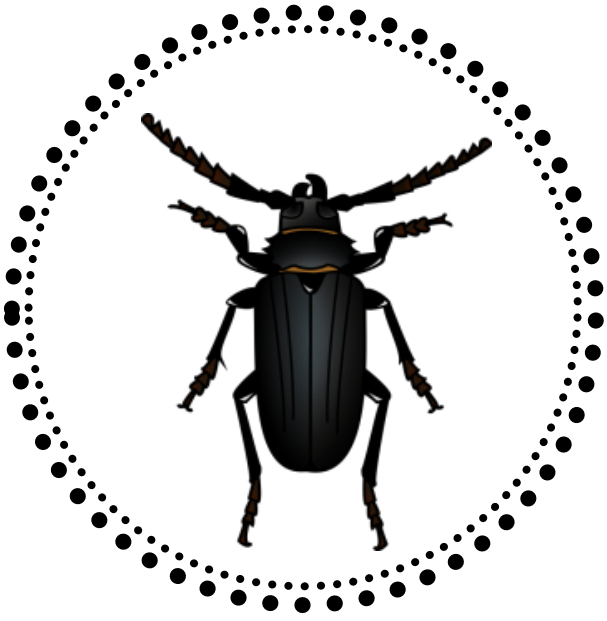

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Explaining population size of the saproxylic beetle *Prionus coriarius* as a function of available dead wood resources

Populationsstorlek av taggbock, *Prionus coriarius*, i förhållande till mängd dödvedsresurser

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ABSTRACT

Dead wood is an important substrate for many forest bound species including the large group of dead wood associated (saproxylic) beetles. Saproxylic beetles have species specific substrate requirements, that may vary according to factor such as tree species, object type, trunk diameter and decomposition stage. In modern production forests, the density of dead wood is much lower than in natural forests, which poses a threat to many saproxylic species that require higher densities of substrate. The minimum dead wood density at which species can sustain viable populations is referred to as the extinction threshold level. In this study, the red-listed saproxylic beetle *Prionus coriarius* was sampled at over 50 sites in Scania, south Sweden, using pheromone trapping. Surveys of dead wood densities were conducted in 38 sites where the beetle was present which allowed for a regression analysis between beetle catch and the dead wood density at a site. Deciduous stumps and damaged trees of minimum diameter 20 cm and intermediate decomposition state could best explain the variation in trap catches. No extinction threshold level of dead wood was detected. Dead wood at a spatial scale of 250 m radius could better explain abundances than a spatial scale at 50 m. GIS data of deciduous forest volume was tested as a proxy for dead wood, but such a relationship was not identified. Since the species can utilize cut stumps, the substrate requirements of *P. coriarius* alone cannot explain that the species is decreasing; dispersal limitation and fragmentation may be the reasons behind its decline in the past century. Several populations are low in number with low levels of substrate and should be boosted by creating more dead wood resources to avoid local extinctions. Clear cuts may serve as temporary habitat, but dead wood continuity must be ensured if the species is going to survive in production forests.

CONTENTS

INTRODUCTION

Modern forest management has caused significant changes to the forest ecosystems in Sweden in the past century. Clear cut harvesting, the standard method used in industrial forestry, is negative for many of the species living in the forest (Müller & Butler 2010). Another reason is that the dead wood availability in a production stand is typically only around one tenth of what is available in unmanaged forests (Dahlberg & Stokland 2004). Dead wood is a key component needed for forest biodiversity: in Sweden around 6000-7000 species are saproxylic, meaning that they depend on dead wood during some part of their life cycle, and of these, around 1260 are saproxylic beetles (Dahlberg & Stokland 2004).

SUBSTRATE REQUIREMENTS

Beetles vary in their substrate requirements according to such factors as tree species, tree diameter, decomposition stage, type of dead wood and sun exposure (Dahlberg & Stokland 2004). For instance, the small longhorn beetle *Poecilium alni* utilizes thin, recently dead oak twigs, which are quickly generated (Ehnström & Axelsson 2002). On the other end of the spectrum, the hollow-dwelling scarabaeid beetle *Osmoderma eremita* has been shown to reach peak population size in the hollows of 300-400 year old oaks (Ranius 2009). The persistence period, the time that a substrate is useful for a specific species, will also differ, where a branch can be utilized for one or a few years before it is spent while a large hollow tree can be suitable as habitat for several decades, see Fig. 1 (Ranius & Hedin 2001). In the production landscape the most rapidly generated substrate will typically be continuously produced during any kind of active management or during a minor natural disturbance such as a storm. Late successional substrates exemplified by hollow trees, however, are largely absent in the modern production forest and occur instead in certain nature forests or woodland pastures. At the intermediate level are objects like mature dead trees, which may take in the order of a century to be generated and which may then be used as substrate for one or a few decades, see Fig. 1. This type of dead wood corresponds to the age of trees when they are harvested. The fate of saproxylic beetles associated with medium level dead wood substrate in production forests is therefore related to how many trees that are left for conservation purposes during clear cut harvesting. It is important to further the current knowledge base of the ecology of beetles dependent on medium-level temporal scale dead wood so that efficient, evidence-based conservation strategies can be developed.

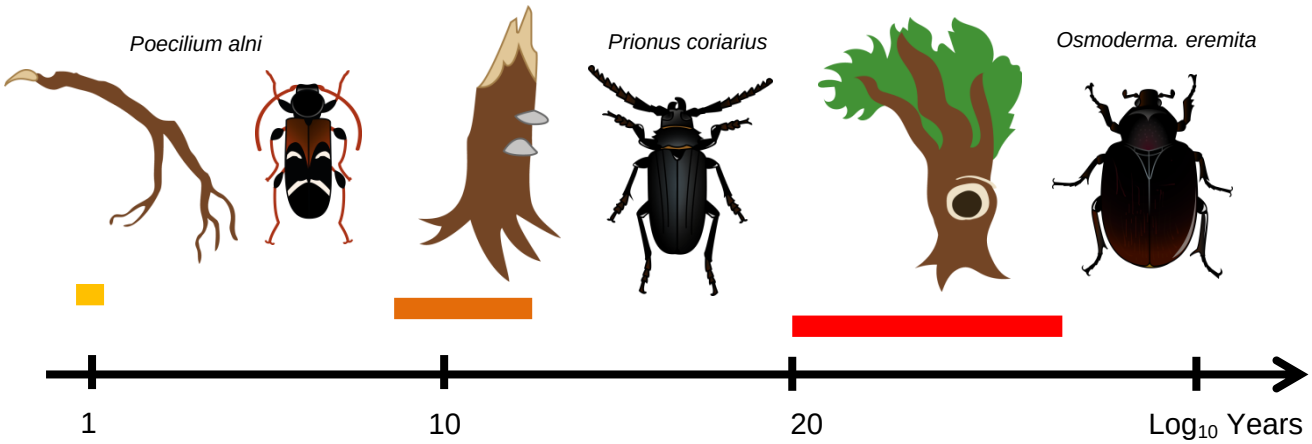

Figure 1: Illustration of the generation time and substrate persistence time of three different types of dead wood on a log time scale. Where generation time refers to the minimum time taken to produce the object of dead wood and substrate persistence time is the period that object can be utilized by a certain species of saproxylic beetle. Example species of saproxylic beetles depending on the different types of dead wood are shown in the figure.

Substrate threshold

In the context of reaching a balance between the economic value of trees and their value for conservation as dead wood, it would be helpful to determine what level of substrate density is sufficient to sustain viable saproxylic beetle population. This substrate level can be referred to as an extinction threshold, and is described by Ranius and Fahrig (2006) as a critical value of habitat density, at which population persistence probability changes rapidly, such that above the threshold the population persists and below the threshold the population becomes extinct, see Fig. 2. Such estimates could be very useful in developing forestry models in line with saproxylic species' substrate requirements. Some empirical studies have been conducted to determine extinction threshold levels. Ranius (2002) studied tree hollow-living beetles and found that the red listed beetles *Elater ferrugineus* and *Tenebrio opacus* were absent from almost all stands of <10 hollow oaks. Økland et al. (1996) collected beetles of 190 species and concluded that eight of these did not occur in areas where the level of dead wood was lower than 8 – 23 m^3 ha^{-1}, corresponding to 3-7 large logs per hectare. This pattern was only detected on a large spatial scale of 1 km^2 or 4 km^2 and not at scales of 0.16 ha or 1 ha.

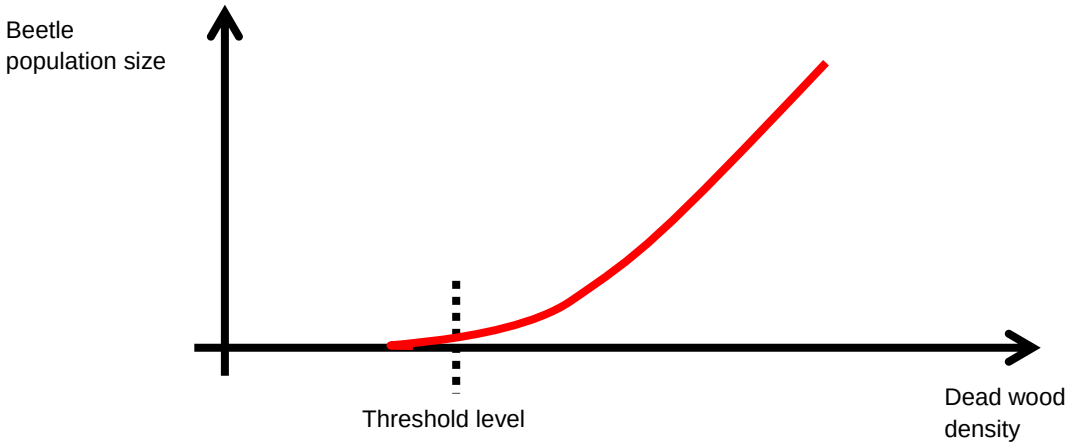

Figure 2: Theoretical sigmoidal response of a beetle population size to increasing density of dead wood, illustrating the concept substrate threshold level. The population size reaches zero at the threshold level of dead wood density.

Dispersal

Not only the type and density, but also the spatial organization of dead wood is of great importance for saproxylic beetle conservation. Different species of saproxylic beetles have variable dispersal ability, thought to depend on the stability and spatial distribution of the dead wood substrate: a species that depends on spatially unpredictable and/or ephemeral substrate would often need to disperse over long distances to locate that substrate, while species depending on stable, commonly found substrate would benefit by staying in the host patch, and select for short dispersal (Nilsson & Baranowski 1997). In one of few available studies, the tree-hollow dwelling beetle species *Osmoderma eremita* was shown to have both a limited rate and range of dispersal: only 15% of adults left the host tree and for those that did, the maximum dispersal range measured was below 200 m (Ranius 2001).

In fragmented forest landscapes, dispersal limited saproxylic beetles become isolated and vulnerable to environmental and genetic stochasticity (Dempster & Mclean 1998). To avoid local extinctions in the long term, habitat patches must occur close enough so that movement between patches is possible (Hanski et al. 1995; Dempster & Mclean 1998). It has been shown for forests in Switzerland that stands with higher connectivity of internal dead wood resources had higher species richness of saproxylic Coleoptera than those forests where the dead wood was clumped into separate pockets (Schiegg 2000). The results of a study in

south Swedish beech forests suggested that red-listed saproxylic beetles were more dispersal-limited than those not on the red list (Brunet & Isacsson 2009).

A saproxylic species' dispersal ability can influence the suitable spatial scale for habitat studies linking environmental variables with population size (Holland et al. 2004). A study where the independent variable, such as substrate density, is surveyed on a large spatial scale will in theory be better fitted to a well dispersing species that can find and colonize habitat substrate over large distances. Inversely, a smaller scale study is more fitting for a species that is dispersal limited and which may have a relict population limited to a few suitable habitat trees. Consequently, a study conducted on an ill-fitting spatial scale is then less likely to get significant results on how a species responds to the density of its dead wood substrate. Some studies have therefore used experimental designs where an environmental variable can be analyzed at several spatial scales. In a Canadian study, Holland et al. (2004) used computer software to determine the characteristic spatial scale of a number of longhorn beetle species using percentage forest cover as the environmental variable. Bergman et al. (2011) used high definition survey data of veteran oak trees in Östergötland, southeast Sweden, to determine appropriate spatial scales for oak-dependent beetles. Both studies found that most species have characteristic spatial scales at which environmental predictor variables are most likely to give statistically significant responses.

The tanner beetle, *Prionus coriarius* (family Cerambycidae) is a potential model species for beetles utilizing medium level temporal processes of dead wood succession. The species is associated with coarse roots of dead, decaying trees, both coniferous and deciduous (Ehnström & Holmer 2007). Theoretically, cut stumps should also be suitable as substrate since the root system is similar to trees that have broken naturally. A species that is able to utilize the roots of cut stumps could be expected to be well suited to a forestry regime dominated by clear cuts where hundreds of stumps are left in the ground. However, *P. coriarius* has had a negative development in the past century and is currently listed as near threatened (NT) in the Swedish Red list (Lindhe et al. 2010; Gärdenfors 2015). One explanation for this is that its substrate requirements are more restrictive than previously thought, perhaps that dead wood is only suitable during a short interval reflecting a certain decomposition stage or that only certain dead wood types are useful. A required threshold level of dead wood could also be required for the species to remain in a habitat patch, above the density typically provided in production forests. Another explanation is that limited dispersal ability is preventing the species from utilizing available dead wood resources in the forest landscape. A landscape study on the species, linking substrate requirements with population size, is a way to further the knowledge basis and provide insight into the mechanisms that are dictating its current decline.

Conducting studies on *P. coriarius* using traditional trapping methods is difficult. In a study on saproxylic insects in Söderåsen national park, where window traps were used to capture saproxylic beetles, the species was not caught even though the site is known to contain one of the largest known populations in Sweden (Brunet & Isacsson 2009). Luckily, *P. coriarius* is one of the species for which pheromone based sampling methods have been developed in the past decade (Rodstein et al. 2009; Barbour et al. 2011). Many saproxylic beetles rely on pheromone chemical cues as a communication tool, in order to localize each other for mating. Technological advances has allowed for the identification and synthesis of the specific pheromones used by certain species. The synthesized pheromone can be used as a sampling tool, allowing for systematic, quantitative measures of population sizes that were previously impossible to attain (Larsson & Svensson 2011).

The main aim of this study is to characterize the substrate requirements of *P. coriarius* and thereby gain insights into the ecology of the species. The main hypothesis is that a significant part of the variation in population size of *P. coriarius* can be explained by available resources of dead wood, defined according to the variables decomposition stage, species, type and diameter. A species' characteristic spatial scale is related to the dispersal ability of population

on the local level. It is hypothesized that the variation in population sizes can only be explained if dead wood is surveyed in an area close to the characteristic spatial scale of *P. coriarius.* The results of a significant relation between population size and substrate density are checked for a minimum threshold level of substrate. Finally a method using deciduous forest volume from GIS data as a proxy for dead wood is attempted.

MATERIALS AND METHOD

STUDY SPECIES

Prionus coriarius (Coleoptera: Cerambycidae) is a blackish-brown beetle that is easily recognized by the long, saw-toothed antennas and its very large size (20-45 mm), see Fig. 3 (Ehnström & Holmer 2007). Eggs are oviposited by the female on basal parts of dead trees; the hatched larvae bore into the wood and proceed down into the roots, which are the main food source (Duffy 1946). If food resources in one root are exhausted the larvae are able to move through the soil to reach nearby roots (Duffy 1946). After 3-5 years the larvae leave the roots for the surrounding soil and construct a cocoon out of soil particles, the size of a chicken egg. The larvae cocoon in early summer and typically emerge as fully formed adults in July-August; males tend to emerge before the females (Duffy 1946). The adult beetles do not feed and have the sole purpose of reproducing; they die after a few weeks. Encountering the species is most likely in the afternoon or at dusk, around the bases of dead or damaged trees (Ehnström & Holmer 2007).

Figure 3: Prionus coriarius, male. Photo by author.

P. coriarius is a generalist that can live on a wide range of tree host species. In southernmost Sweden it is most typically found on beech (*Fagus sylvatica*), which is the most abundant deciduous tree in this part of the country (Ehnström & Holmer 2007). North of the range of beech, Scots pine (*Pinus sylvestris*) is the most common host species. The species is able to utilize the roots of most deciduous Swedish tree species and Duffy (1911) described the species as polyphagous, with little discrimination in the choice of tree based on species. Ehnström and Holmer (2007) suggest that the prime habitat of the tanner beetle in Sweden has probably been in pastures with scattered solitary oaks and beeches, as well as in sparse stands of Scots pine in sandy areas. The distribution range of *Prionus coriarius* in Sweden is largely coastally-bound, occurring only in the southern part of the country, see Fig. 4. The species also occurs in Denmark, the Baltic states, England, and Central and Southern Europe (Ehnström & Holmer 2007).

Figure 4: P. coriarius has a southern coastally bound distribution. All findings of P. coriarius reported to the Swedish species gateway up to December 2015. Image from http://artfakta.artdatabanken.se

Based on historical findings in the past century, *Prionus coriarius* population indices were found to have significantly decreased (Lindhe et al. 2010). The species is currently listed as near threatened in the 2015 edition of the national Red List. There is a current and expected loss of population due to a loss of habitat and increased fragmentation of habitats

(Gärdenfors 2015).

STUDY AREA

In total 57 sites where included in the study. Site selection was primarily based on the results of an unpublished study (Larsson et al 2012, unpublished) on the distribution of *Prionus coriarius* in Scania. The large majority of sites where *P. coriarius* was found were included in this study and extra sites were added where it was thought likely that the species could be found, as well as some from findings reported on the Swedish Species Gateway (http://www.artportalen.se). In order to keep sites independent from each other there was a minimum distance of 1000 m between sites. This could not be fulfilled in all cases; the sites Maglehems Ora and Ravlunda West were placed around 700 m apart.

BEETLE TRAPPING

Traps were constructed using two custom-made black plastic cross-veins, 20 x 25 cm (Industriplast/Nordic Plastic Group, Trelleborg, Sweden) combined with simple plastic components bought at a utility store: a funnel, lid, and a screw-on wide-mouthed bottle with a 4 cm hole drilled through the lid to accommodate the funnel. These were drilled and sawed so that they could be assembled using tie wire and cable ties**.** A GRIPPIE plastic ziploc bag (6 x 4 cm) with dilute pheromone was hung on the assembled trap on-site. Propylene glycol was used as a killing agent. Assembled traps are shown in Fig. 5a-b**.** Male *P. coriarius* are attracted to the trap by the pheromone compound, some fly into the cross veins and drop down into the bottle with the killing agent.

Prionic acid (3, 5-dimethyldodecanoid acid) is the sex pheromone produced by the female of the North American species *Prionus californicus* (Rodstein et al. 2009). This substance has been shown to also attract males of several congener species, including *P. coriarius* (Barbour et al 2011). The synthesized chemical was obtained from Jocelyn Millar's research group (University of California, Riverside). Concentrations of 100 in 500 µl isopropanol were used in each trap.

The pheromone traps were placed in areas with objects of dead wood. Three traps were placed at each site, configured as an isosceles triangle with a distance of 100 m between traps, see Fig. 6a-b. For certain sites this configuration was problematic due to physical obstacles like river ravines. In these cases the traps were placed as close to the ideal configuration as possible. Traps were hung from branches at heights between 1-2 m; higher where protection was needed from grazing cattle. The catches were not expected to depend on the height of the traps.

For each trap two qualitative parameters were estimated so that it could be tested if trap placement had an effect on the number of caught individuals. Any disturbance around the trap that could hinder beetles from reaching the trap was noted (Yes/No). Canopy cover was recorded on a scale with three categories, where 1 was completely open with no or insignificant canopy cover, 2 was semi-open and 3, with complete canopy cover.

Traps were up and baited between 24 July and 29 September 2015. Traps were emptied and dismantled 31 August - 29 September. Surveys of dead wood were carried out between 30 July and 31 October.

Figure 5 (a) Assembled pheromone trap (b) Trap hanging in beech high stump at the site Snogeholm. Photos by Mikael Molander and author.

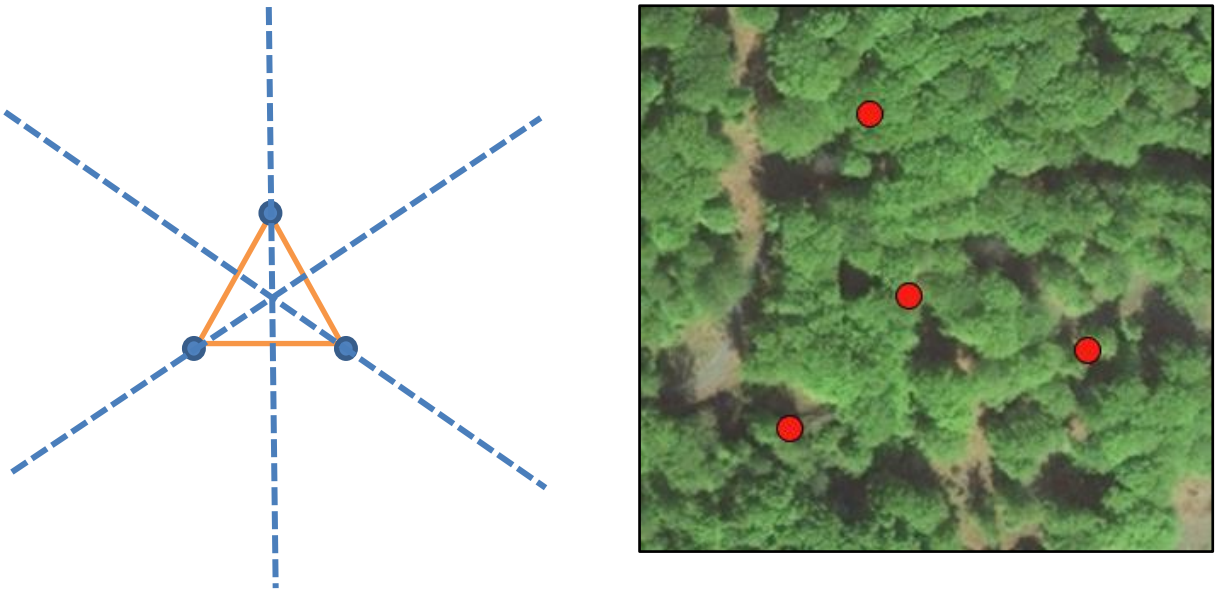

Figure 6: (a) Diagram of a site configuration. Blue circles represent traps, situated in a triangle (orange) with 100 m between traps. Dashed blue lines represent the 500m transects surveyed for dead wood (b) Plotted trap and centroid coordinates for site Ravlunda Skjutfält

SUBSTRATE SURVEY METHOD

At each site dead wood was surveyed along three 500 m transects, each passing through the site centroid as well as one trap, so that all transects overlapped in the centroid, see Fig. 6a. Walking along a transect, all objects were recorded in a band 20 m wide centered on the transect. The transect design created an overlap of the three transects in the site centroid, which meant that dead wood objects in that area would be oversampled. This was accepted, given that the overlapping area made up only a small portion, around 2%, of the total surveyed area at a site. The dead wood objects were categorized according to Table 1. For each object, diameter, species and decay stage was recorded, according to Table 2. See Fig. 7 for photographs of representative beech high stumps of each decay stage.

Table 1: Object types of dead wood recorded during substrate surveys

High stumps	Tree stumps of minimum 1 m height,
Natural stumps and Cut stumps	Stumps below 1 m, distinguished by if they seemed to have had fallen naturally or been cut by a machine
Standing dead trees	Tree that has died without snapping off like a high stump
Uprooted trees	Downed tree with part of the root system in connection with the ground
Trees dead at base	Trees that were alive but damaged or partially dead at the base

Table 2: Variables recorded per dead wood object during substrate survey

Diameter of the trunk	For objects that were tall enough the diameter was taken at breast height (1.3 m), for lower objects the diameter was taken where possible.
Tree species	Dead wood objects determined to genus level. Objects which could not be determined were recorded as Unknown.
Decomposition stage, estimated on a four-level categorical scale, adapted from (Ehnström & Holmer 2007):	1: Fresh or recently dead wood, showing no or very little damage to the bark, bark hard.
	2: Lower intermediate decomposition: showing some damage from woodpeckers, fungal attack, slight general degradation. Bark still mostly attached and wood generally intact and hard.
	3: Higher intermediate decomposition: wood quite damaged and degraded, most of the bark gone, wood starting to go soft in many places.
	4: Late stage decomposition: Wood very decayed, all of the bark and much of the wood is gone, wood soft in most places.

The main purpose of estimating decomposition stage was to find a proxy for when the substrate is most suitable for the study species. Since the target species utilizes the roots, it was assumed that the general state of the visible tree would in turn reflect the decay stage of the roots. Decomposition stage is a difficult parameter to standardize since the speed and the characteristics of decay stages across dead wood types and tree species will differ to a great extent. For example a downed tree has much more ground contact and therefore higher moisture content than a high stump and will decay faster (Dahlberg & Stokland 2004). Consequently, depending on object type the same decay stage will occur at various time intervals after death.

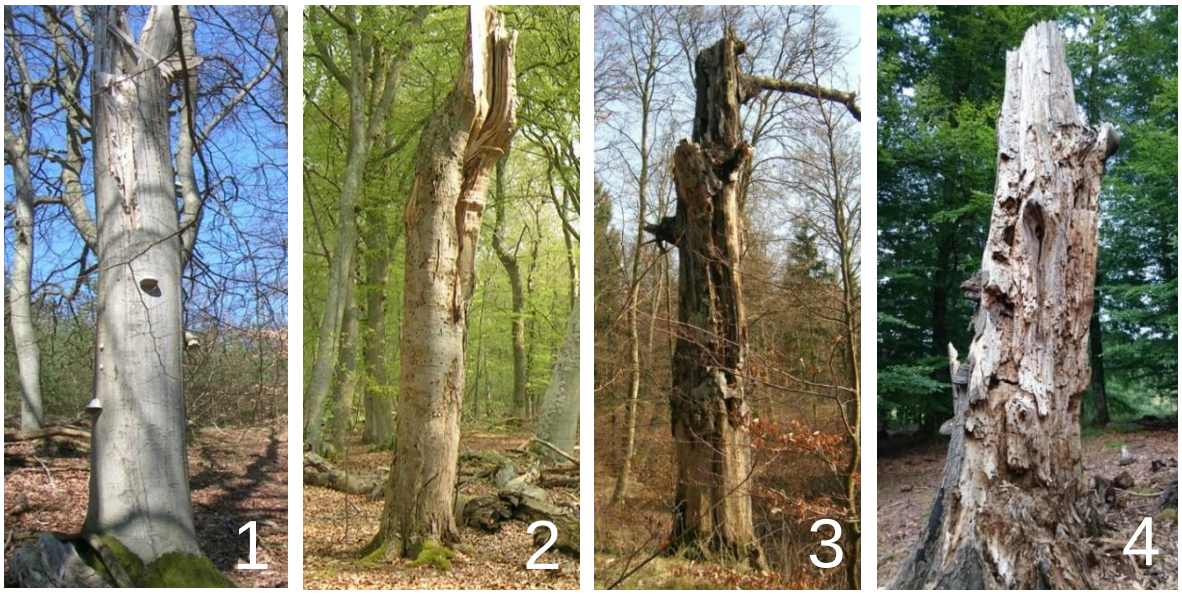

Figure 7: Beech high stumps of decay stages 1-4, starting from left. Photos by Mikael Molander and author.

Statistical analysis

Regression analysis was the main statistical test used to analyze the data, where each site became a point with the number of beetles caught on the Y-axis and dead wood density on the X-axis. Two separate regression analyses were conducted, one using the data from the manual dead wood surveys and the other using GIS-data of deciduous forest volume. For the analysis using dead wood survey data, two different spatial scales were used separately. At the most local level, called dead wood trap scale, the catch of each trap was plotted against the density of dead wood surveyed in the 100 m transect section that passed through the associated trap, see Fig. 6a. At dead wood site scale, all three 500m transects at a site were included, pooling the results against the mean beetle catch of the three traps at the site.

The analysis based on GIS-data used deciduous forest volume as the independent variable (SLU Forest Map, Dept. of Forest Resource Management, Swedish University of Agricultural Sciences). The total volume of deciduous forest was extracted around each site centroid in circular plots of radius 250m, 500m and 1000m.

For statistical analysis the software programs Microsoft Excel and SPSS were used. For GIS analysis QGIS and ArcGIS were used. Statistical significance was defined as p=0.05.

Results

Catches

Prionus coriarius was caught in 49 out of 57 sites, with catches recorded in a total of 130 traps. Four traps had fallen down so that catches could not be recorded, three of these occurred in sites that had recorded catches in at least one other trap. The maximum catch at a single site was 605 individuals, caught at Hallands Väderö. The minimum number was 1 individual caught, in St Olof, Nällåkraskogen and Sövdesjön Ranås. The median number of caught individuals per trap was 13 (including zeroes at sites with caught individuals). The mean number of caught individuals per trap was 25.3. Six sites had mean catches exceeding 50 individuals. The distribution of catches can be seen in the map in Fig. 8. The average number of caught individuals per site is shown in Fig. 9a (see Table 1 in Appendix 1 for detailed account of catches).

The coefficient of variation (CoV) at a site, expressed as the standard deviation of catches divided by the mean catch, is a measurement of the degree of homogeneity between the three trap catches at each site. The coefficient of variation of the 49 sites were the species was caught is plotted in Fig. 9b. The lowest SD/mean was 0.023, describing site Ravlunda West with catches 66, 68, 69. The highest SD/mean, 1.73, represented the site Bellinga West Forest with catches 0, 0, 7. The overall CoV is generally interpreted as low, which signals that the traps had relatively homogenous catches. Overall the traps with the highest CoV were those with very few caught individuals where one of the traps had a zero. These values for CoV are slightly misleading in that the absolute difference between catches were only very few individuals, but in relative terms the CoV becomes high. The three traps with catch distribution 1, 0, 0 get a very high CoV, which does not describe that catch well, which is why these are highlighted in Fig. 9b.

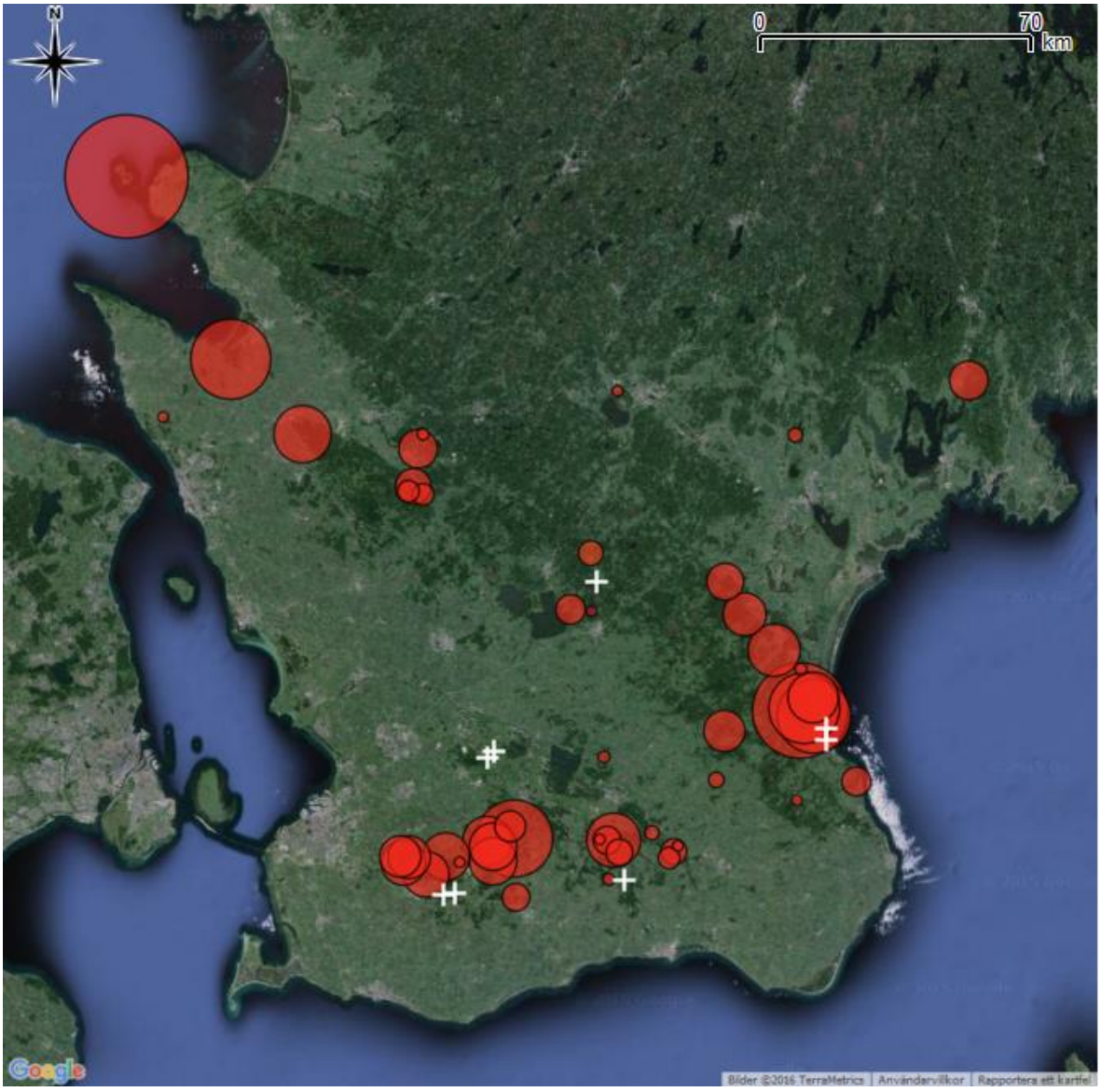

Figure 8: Map of Scania displaying all sites included in the study. Sites with catches of P. coriarius are shown as red circles, size-scaled after the mean catch at the site. Sites with no catches are shown as white crosses.

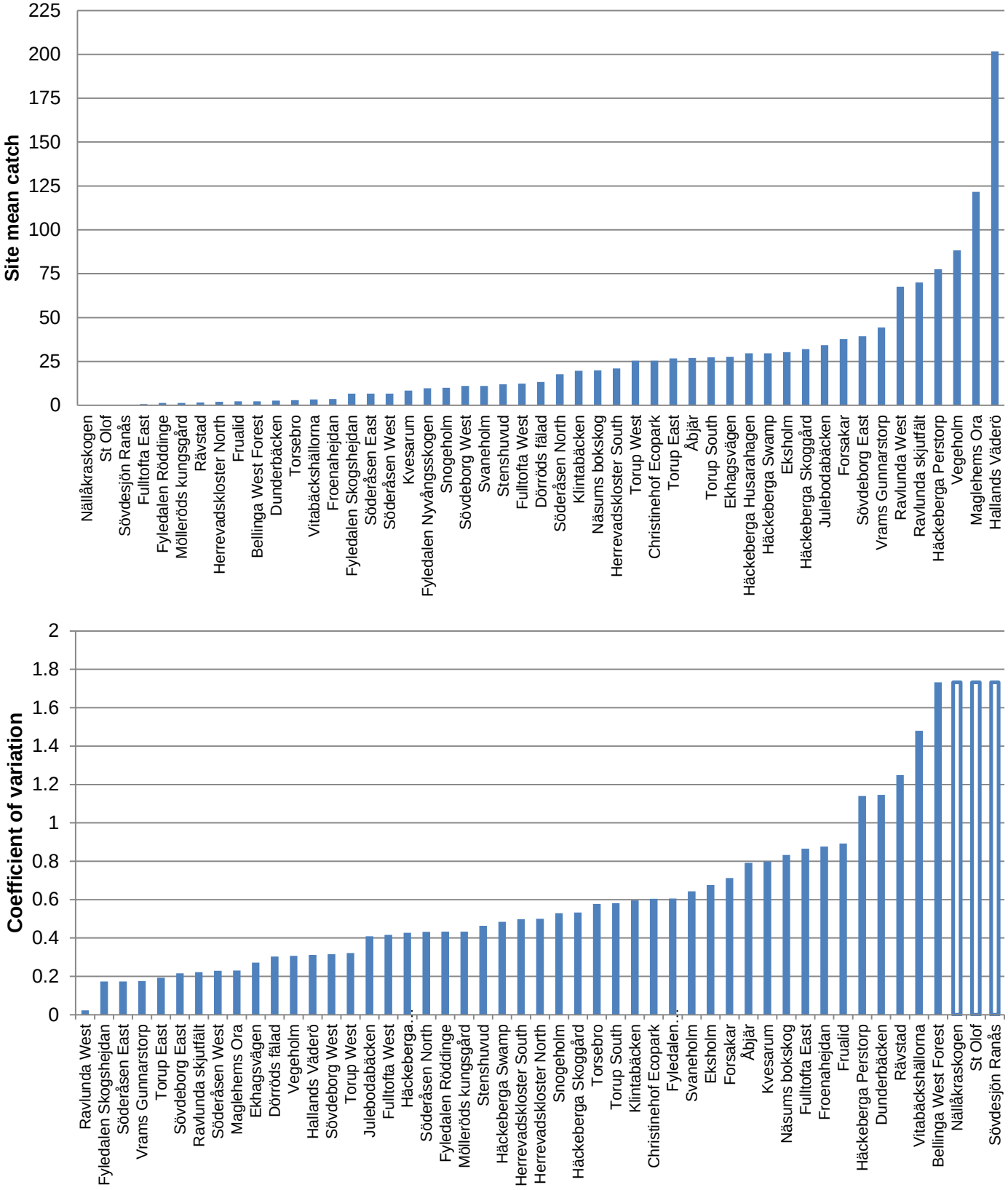

Figure 9 (a) Mean catches of P. coriarius per site, omitting sites with no caught individuals (b) Coefficient of variation of catches. The three sites with the highest value of CoV are left white to mark that they had catch distribution 1, 0, 0 which does not truly signify a heterogenous catch.

Dead wood

Out of 57 sites included in the study, 43 were surveyed for dead wood and out of these, 38 had catches of *P. coriarius*. The sites with catches that were not surveyed were omitted either because of a difficult terrain or due to lack of time. The sites without catches that were surveyed were done so before the trapping period ended when final catches were unknown.

3861 objects of dead wood were recorded in the 44 sites with recorded catches. The most frequently recorded deciduous tree species was beech (*Fagus sylvatica*) followed by birch (Betula spp.) and oak (Quercus spp.), see Fig. 10. Trees making up less than 1% of the total were collected into the category “Other deciduous”. Coniferous species were grouped into one category, which made up 28% of objects recorded. 13% of the total objects could not be identified to genus level and were recorded as “Unknown”.

The most common object type was the Cut stump which made up more than half of the counted objects, see Fig. 10. Natural stumps were the second most counted objects followed by High stumps. 93% of unknown objects were either cut stumps or natural stumps. Objects of decomposition stages 1, 2 and 3 were quite evenly sampled having 21-22% of the total each, while stage 4 had 36% of the total.

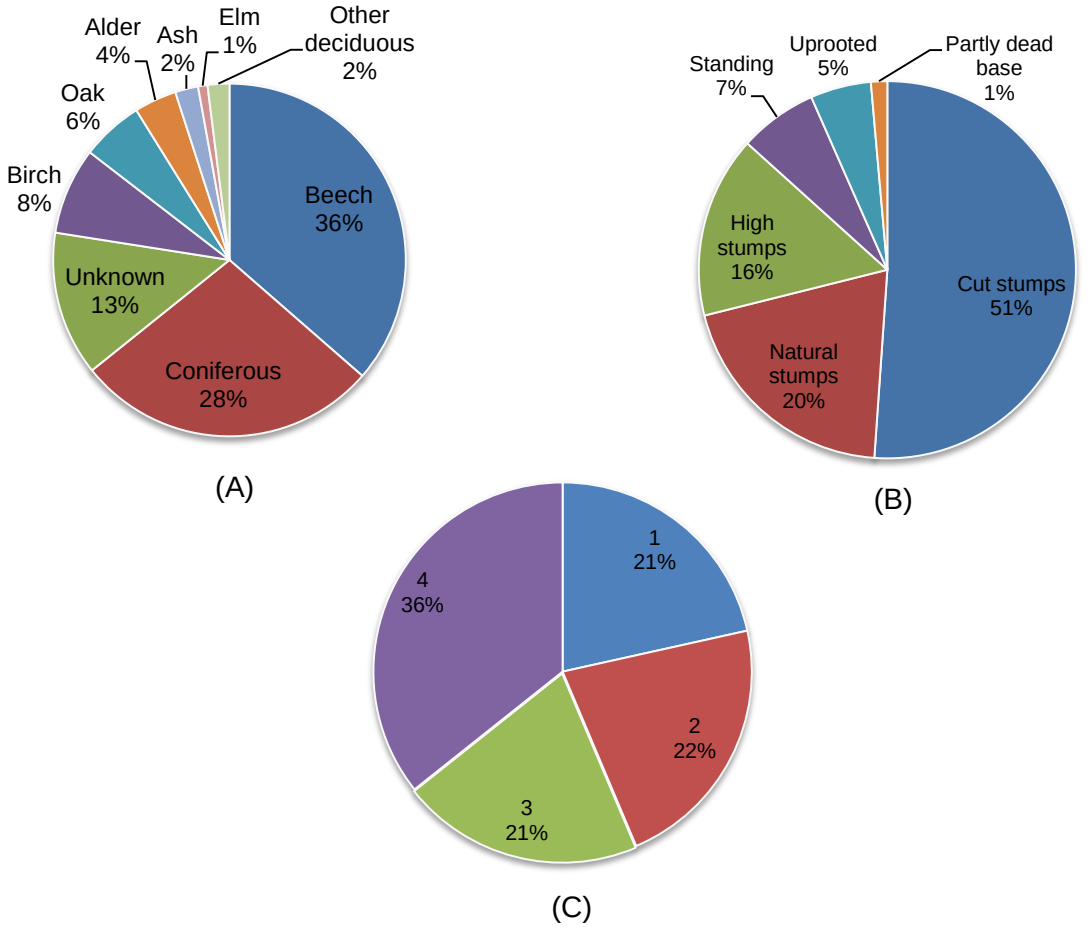

Figure 10: Pie charts summarizing total surveyed dead wood according to distributions of (a) tree type, (b) object type and (c) decomposition stage. For precise definitions of object types and decomposition stages see Materials and Method.

REGRESSION - SITE SCALE

Regression analysis was conducted to correlate dead wood resources with the mean catch of beetles at each site. This analysis included all 38 localities where dead wood resources had been surveyed. Sites that did not appear to host a population were excluded, because the absence of beetles could be due to prior extinction events without possibility for re-colonization, which may be unrelated to the present amount of available habitat resources.

Multiple regression was attempted, with the intention that certain categories of dead wood that best explained the variation in population sizes would be identified and the relative importance of different factors could be determined. This approach was not successful: the software selected only one such category in the final model and when plotted it was clear that it was not a strong predictor variable. Instead, simple regression was performed where the strongest correlation was identified through a step-wise manual procedure where the effects of different dead wood factors where tested by including or excluding these in the dead wood independent variable.

Starting off, all objects of dead wood were included in the regression, which gave a significant correlation at $p<0.05$ ($p=0.0472$, $R^2=0.105$), see Fig. 11. Then progressive exclusions of data objects based on diameter, decomposition stage, tree species and object type were done to determine what selection of substrate factors could best explain the population size of *P. coriarius*. Limiting the diameter of dead wood to objects larger than 20 cm produced a marginally more significant correlation than including all objects ($p=0.0458$, $R^2=0.106$), see Fig. 11. Increasing the cutoff diameter to 30 cm lowered the significance to almost corresponding values as the full set of objects. Further increasing the diameter to 40 cm decreased the significance of the correlation to just below significant levels.

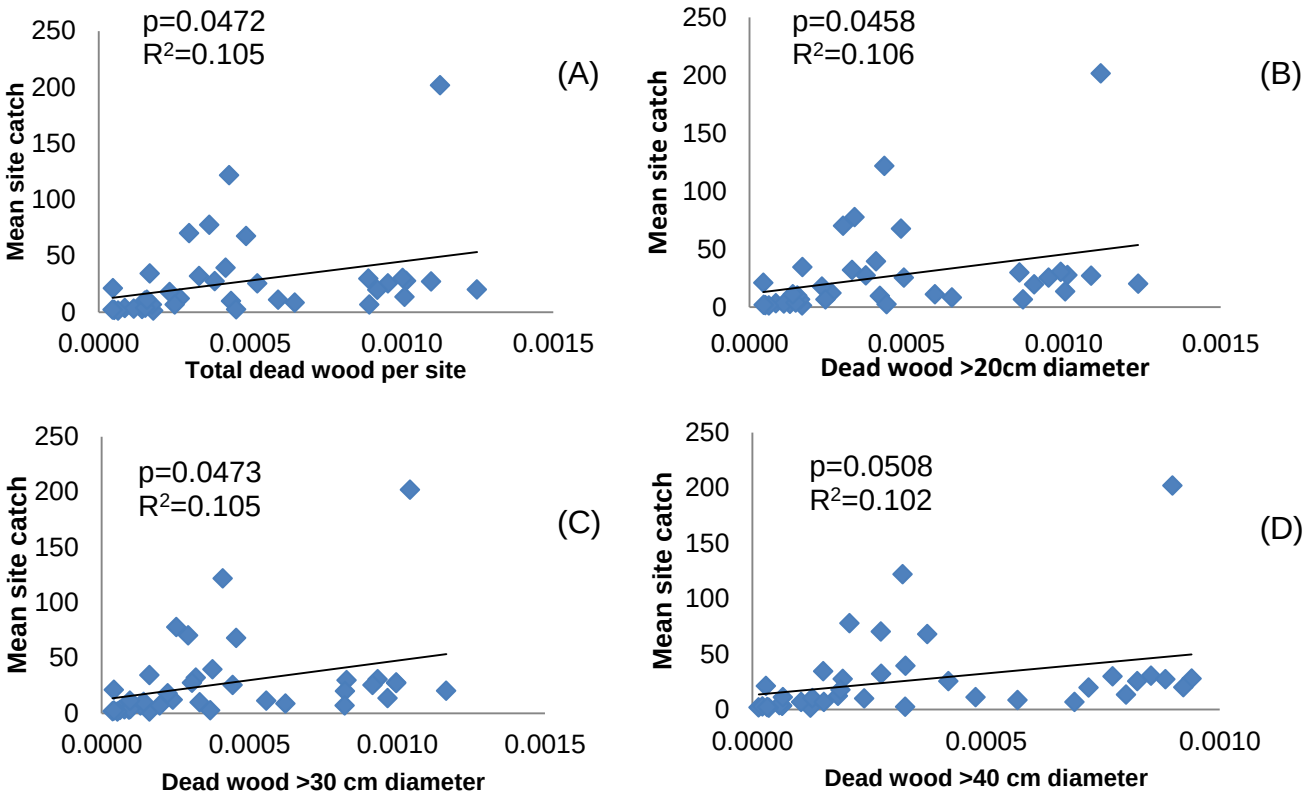

Figure 11: Plots of mean catch of P. coriarius against amount of dead wood in m^2 area dead wood per m^2. Data selection based on diameter of dead wood objects.

When looking only at dead wood objects of a certain decomposition stage, stages 2 and 3 , plotted separately, gave correlations at a significant level (p=0.0132, R^2= 0.159 and p=0.00585, R^2=0.193, respectively), see Fig. 12a-b. Dead wood at decay stages 1 and 4 were not significant. Combining all dead wood at stages 2-3 gave the strongest correlation when looking at decomposition stages (p=0.00184, R^2=0.239), see Fig. 12e.

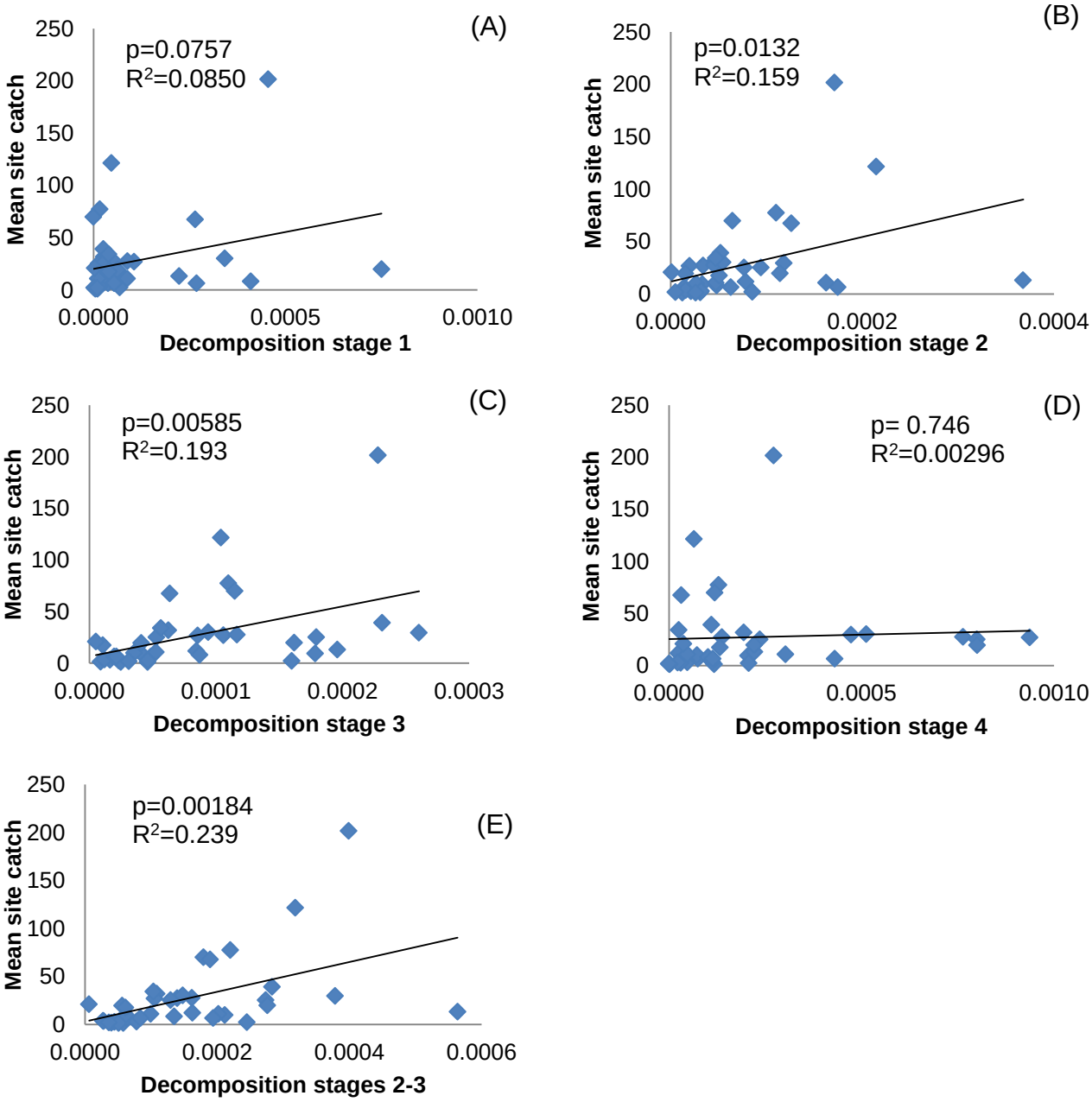

Figure 12: Plots of mean catch of P. coriarius against amount of dead wood in m^2 area dead wood per m^2 area transect. Data selection based on dead wood decomposition stage.

Excluding all coniferous objects from the regression gave a slightly stronger correlation compared to using all data (p=0.035, R^2=0.118), see Fig. 13a. Further exclusion of all objects characterized as “Unknown” gave the strongest correlation in this section (p=0.0096, R^2=0.172), see Fig. 13b. Only including beech or oak/beech did not give a statistically significant correlation, whereas adding birch gave a significant result (p=0.0249, R^2=0.132), see Fig. 13e.

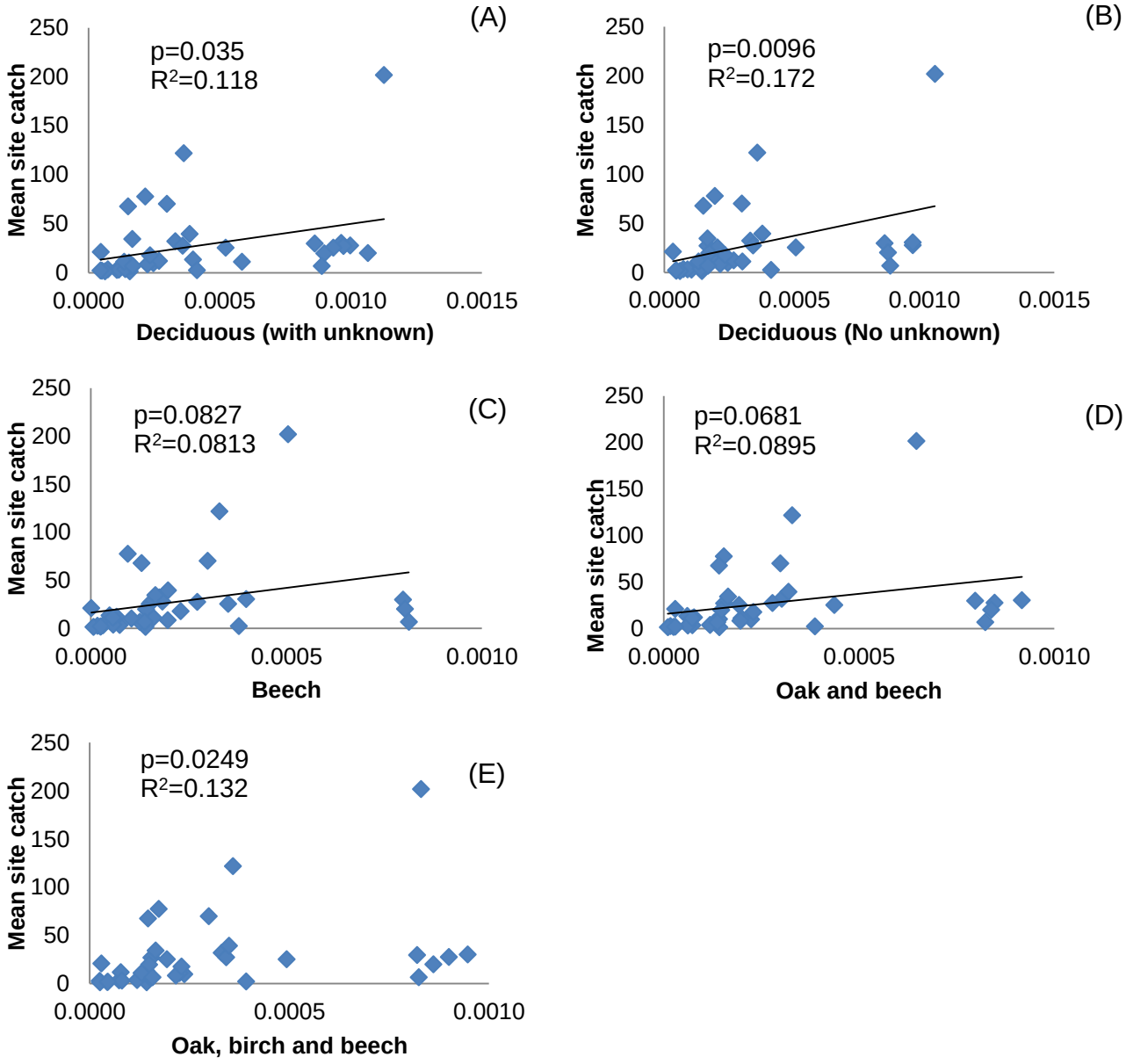

Figure 13: Plots of mean catch of P. coriarius against amount of dead wood in m^2 area dead wood per m^2 area transect. Data selection based on dead wood tree species.

Out of the different objects measured, isolating all high stump objects showed a highly significant correlation with mean catch, see Fig. 14d. Other types of stumps did not give a significant correlation (all stumps, natural stumps and cut stumps), Fig. 14a-c. Grouping the remaining categories of dead wood, standing dead trees, uprooted trees and trees that were damaged at the base, gave a significant correlation, see Fig. 14e.

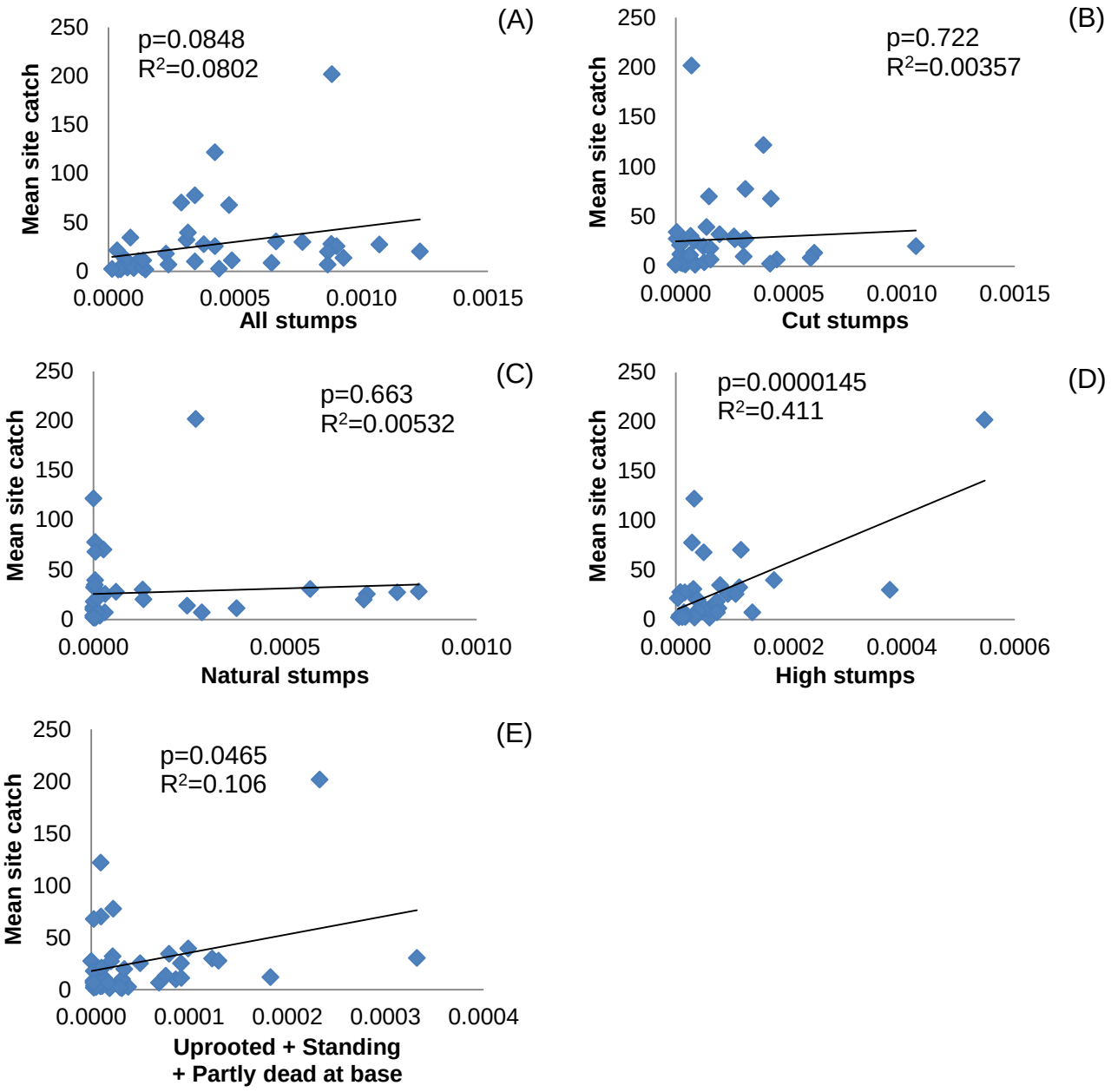

Figure 14: Plots of mean catch of P. coriarius against amount of dead wood in m^2 area dead wood per m^2 area transect. Data selection based on dead wood object type.

Combining the most significant correlations from each of the previous sections into one plot gave the correlation of all deciduous high stumps, excluding unknowns, of diameters above 20 cm and in decay stage 2-3. This correlation was significant, although less so than using all high stumps, see Fig. 15c. Testing fewer of the factors in the same correlations gave variable results, never improving on the original high stump correlation in Fig. 14d, see Fig. 15.

Expanding on the selection and using all types of stumps (cut stumps, natural stumps, high stumps) of decomposition 2-3 dramatically improved on the non-significant plot in Fig. 14a using all stumps, ($p=0.0005$, $R^2=0.292$). Removing all coniferous trees and unknown objects further increased the strength of the correlation ($p=0.00000728$, $R^2=0.432$). The strongest correlation of all was found by taking all deciduous (excluding unknowns) stumps (cut stumps, stumps, and high stumps) and living trees that were partly dead at the base, of diameter >20 cm and in decay stages 2-3 ($p=0.00000306$, $R^2=0.458$), see Fig. 15f.

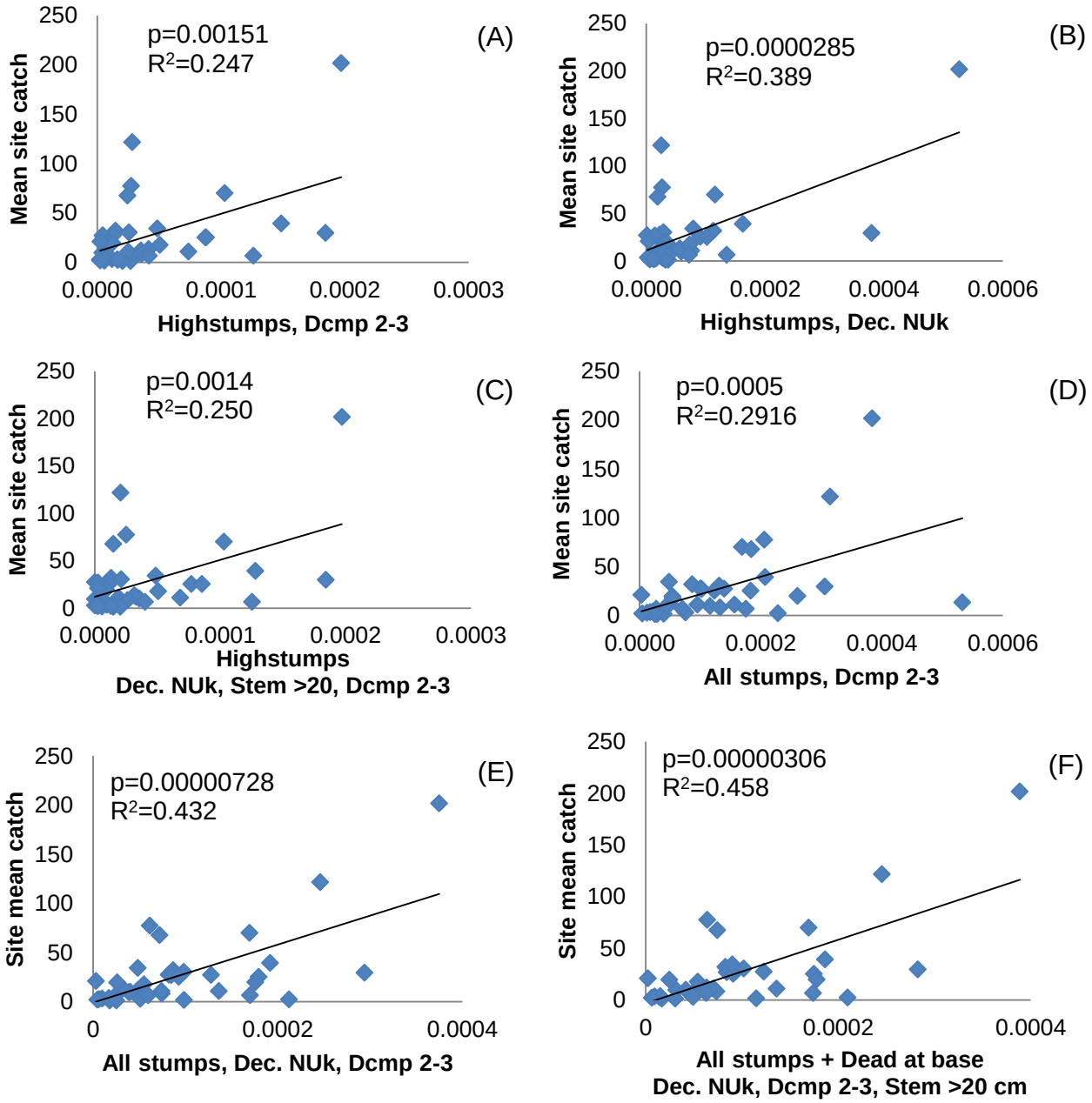

Figure 15: Plots of mean catch of P. coriarius against amount of dead wood in m^2 area dead wood per m^2 area transect. Combinations of dead wood factors which had previously proven significant explaining P. coriarius abundance. Final plot of highest statistical significance in bottom right corner. Acronyms: Dec= Deciduous, NUk= No unknown tree species included, Dcmp= Decomposition stage,

The site Hallands Väderö had both the highest density of substrate and the highest mean catch of *P. coriarius*. As such, certain regression plots may have been over-relying on a single data point for achieving statistical significance. When removing the data point from the correlation using all high stumps, the correlation becomame insignificant and the R^2-value dropped from 0.41 to 0.02 (see Fig. 14d and Fig. 16a). In this instance it became clear that this correlation was too dependent on the Hallands Väderö data point. When removing the Hallands Väderö datapoint from the plot in Fig. 15f, the correlation was still significant but lost half of the explanatory power (p=0.00474, R^2=0.2063), see Fig. 16b.

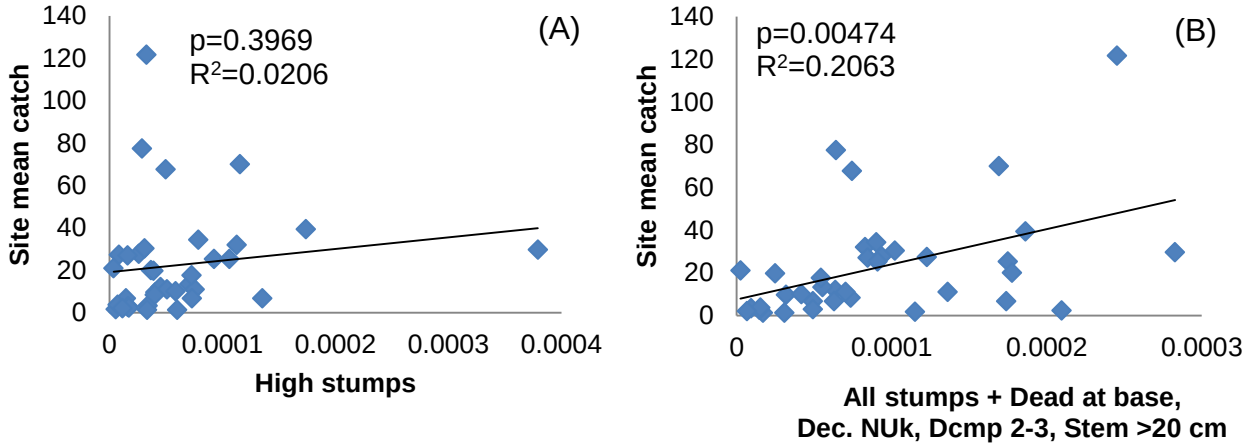

Figure 16: Plots of mean catch of P. coriarius against amount of dead wood in m^2 area dead wood per m^2 area transect. A) The same plot as in Fig. 15f but with the data point Hallands Väderö omitted. B) The same plot as in Fig.14d with the data point Hallands Väderö omitted. Acronyms: Dec= Deciduous, NUk= No unknown tree species included, Dcmp= Decomposition stage

Regression - Trap scale

At the scale of 100 m (50 m radius) transects near individual traps, no regression between catches and dead wood resulted in statistical significance, see Fig. 17. Closest to significance was plotting trap catch against high stumps, see Fig. 17d, although the R^2-value was low also in this case (p=0.120, R^2=0.0223).

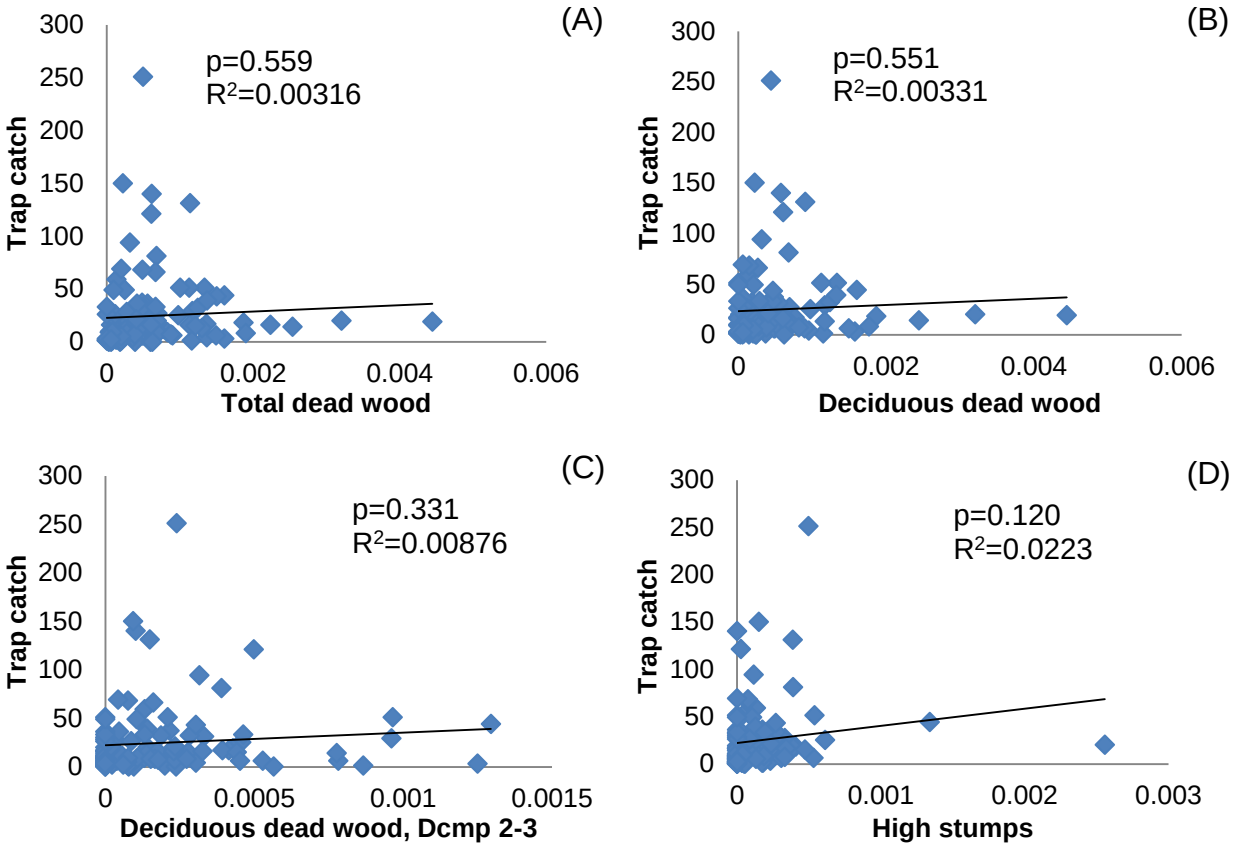

Figure 17: Plots of trap catch of P. coriarius against amount of dead wood in m^2 area dead wood per m^2 area transect. Combinations of dead wood data selection based on several variables combined.

Regression – Deciduous forest volume

When comparing trap catch against the standing volume of deciduous forest at the landscape scale both the 250 m and 500 m levels gave strong significance, see Fig. 18a-b. However the positive trend is entirely caused by the data point representing Hallands Väderö. Taking that data point away renders the regression plots non-significant.

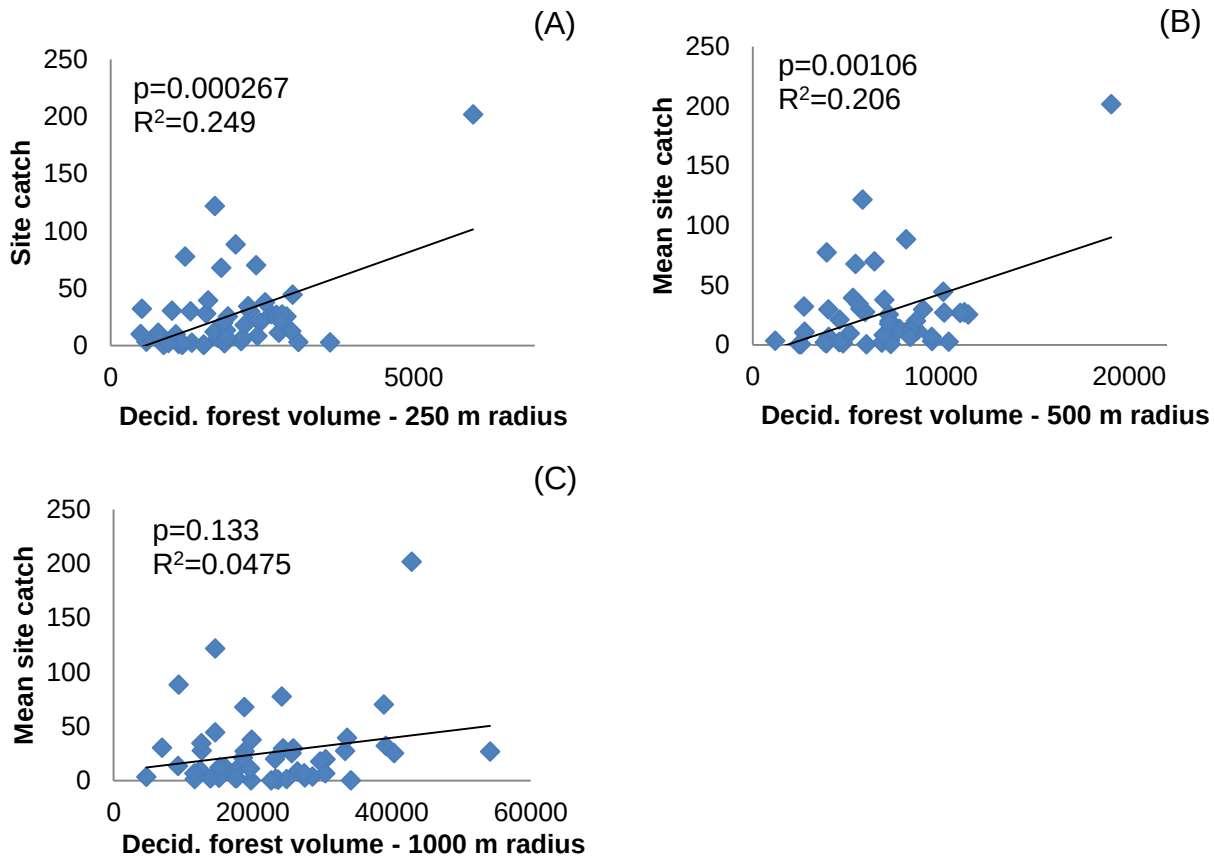

Figure 18: Plots of trap catch of P. coriarius against deciduous forest volume in m^3 per m^2. Deciduous forest volume is measured at different spatial scales around the site centroid trap, with centroid 250 m, 500 m and 1000 m.

Interactions with canopy cover and trap interference

To test if there were significant effects of the placement of traps on the catch relative to the site, nested ANOVA tests were performed for the parameters canopy cover and trap interference. The results of this test gave no indication of that these factors influenced trap catches to a significant degree (interference: p=0.565, F=0.334, exposure: p=0.992, F=0.008).

DISCUSSION

CATCHES

There is a large span of catches, between 1 and 605 caught individuals and between mean catch 25.3 and the mean 202 caught individuals at Hallands Väderö. Overall many populations are quite small while there are a handful of very large populations. Large catches appear to be clustered in certain regions: an eastern area with large populations at Ravlunda Skjutfält and Maglehems Ora and a few very large, seemingly isolated populations in the northwest: Hallands Väderö, Vrams Gunnarstorp and Vegeholm. There is a southern belt of several larger wooded areas such as Torup and Häckeberga that mostly have intermediate size catches. Scattered throughout are small populations such as Mölleröds Kungsgård and Froenahejdan, see Figs. 8 and 9a.

At some sites the distribution of catches can be explained based on how the traps were placed in relation to observed dead wood resources. In the site Vitabäckshällorna, the catches were 9, 1, 0. In this site the trap with 9 caught individuals was located close to several large high stumps in a tree stand separated by an open meadow to the tree stand where the other two traps were located and with a lower level of dead wood. It could therefore be gathered that the first stand had a small population of *P. coriarius* which likely wasn't established in the second stand.

In Bellinga West Forest, the catches were 7, 0, 0 which cannot be explained by the observed or recorded dead wood distribution, although it is possible that a cluster of dead wood had been missed, since parts of the site were difficult to oversee. The site was varied but mostly closed canopy forest, mixed with patches of thick undergrowth. At the opposite end of the spectrum is Ravlunda West, with the lowest coefficient of variation and catches 66, 68, 69. This site was quite open, with the traps located along the edges of a clear cut, in a sparse beech stand. It is possible that the flying patterns and local spatial distribution of male *P. coriarius* varies in response to the configuration of open areas contra closed forest. Although, canopy cover did not have an effect on catches on a trap basis, which could then have been expected.

Häckeberga Perstorp had a catch distribution that is difficult to explain. The catches in two traps were 140, 15, which gives one of the higher coefficients of variance. The third trap had fallen down before being emptied, however the site was inspected shortly before emptying and at that time the third trap had an intermediate catch somewhere in the range of 50-70 beetles. The trap with 140 beetles was placed in a birch pasture adjacent to a spruce clear cut while the other two traps where placed close to thick trunked beech high stumps in a semi-closed mixed deciduous forest stand. Intuitively the trap in the birch pasture would have had the lowest catch as it was the furthest from the assumed substrate, the beech high stumps. As this was not the case, a possible explanation was that the spruce clear cut acted as habitat. However, spruce has not been specified as substrate in the literature on *P. coriarius* (Ehnström & Holmer 2007; Duffy 1946). A possible explanation could be that spruce may be only suitable as substrate only under unique circumstances, perhaps in a short time-window or for a very large diameter of wood, so that substrate utilization in general is rare. Another explanation can be that male *P. coriarius* have unpredictable movement or patrolling patterns when searching for females that happened to pass close to the birch pasture trap.

Maglehems Ora had the second highest catch, suggesting a large population of *P. coriarius*. This site was interesting in that the forest itself was a production beech forest with low to average levels of dead wood in the form of 3-4 high stumps, but the catch was the second largest out of the sites studied. A possible explanation in this case was that *P. coriarius* had colonized the cut stumps of an overgrown beech clear-cut adjacent to the forest stand which acted as the main substrate source.

Dead wood spatial scales

A significant regression between beetle catches and substrate density was only found at the larger spatial scale of 250 m radius. This was in line with the hypothesis that a response would only be found using dead wood surveyed close to the characteristic spatial scale of the species. However, two factors hinder a direct comparison between the spatial scales used. First, the size of the surveyed area to the imagined circular area sampled differed. At trap scale the survey covered around 25% of the 50 m radius circle around the trap, at site level the combined three transects covered around 15% of the 250 m radius circle from the site centroid. Since site scale had a superior explanatory power that result is only strengthened given that a smaller area was sampled. A second issue is that catches at trap level were analyzed as independent, although traps in the same site may have been interdependent. However, had trap scale been the most fitting scale then each trap should in theory be independent of the other traps at the same site, so this is accepted.

The conclusion is that the site scale was suitable when studying *P. coriarius*. However, other studies have been able determine suitable spatial scales more precisely. With substrate spatial data covering a larger area, it can be determined when a species has the strongest response to the environmental data input (Bergman et al 2011; Holland et al 2004). This was not possible in this study as the surveying work was very time-consuming and it would have been difficult to increase the survey coverage further. Still, this study has been able to demonstrate the importance of using appropriate spatial scales to demonstrate significant responses between catches and dead wood density.

Deciduous forest volume

Although two of the spatial scales (250 m and 500 m) of deciduous forest volume against *P. coriarius* catch gave significant results (Fig. 18a-b) these results were misleading and highly dependent on one data point and no overall trend could be identified. The conclusion is that deciduous forest volume is not a good proxy for dead wood abundance, at least in this case. In a primary or old growth forest it is possible that forest volume would have worked better as a proxy but since a majority of forests today are managed, dead wood levels are likely more dependent on management type than on forest tree volume. It has been shown that intensively managed oak forests have significantly lower mean levels of dead wood compared to extensive or multi-use management types (Paletto 2013). Holland et al (2004) were able to successfully use data of forest cover as proxy for dead wood to determine the characteristic spatial scales for 12 species of saproxylic beetles; only one of the species studied did not respond. Although forest cover is not directly comparable to forest volume, the study by Holland et al. illustrates that readily available spatial data can be useful in determining species' characteristic spatial scale, at least for certain species, or within limited areas that are uniformly managed.

Relationships between substrate density and population size

Substrate requirements of *P. coriarius*

At sites where *Prionus coriarius* is present, there is a positive relationship between density of suitable deadwood resources and population size. Similar trends have been found between density of coarse deadwood resources and saproxylic species richness (Økland et al. 1996; Gibb et al. 2006; Franc et al. 2007). The combined regression model that could best explain abundance of *P. coriarius* includes all types of deciduous stumps and living damaged trees of diameter >20 cm and intermediate decomposition levels 2-3, see Fig. 15f. These results are in line with the stated hypothesis: that substrate availability is a significant predictor for population size of *P. coriarius*.

P. coriarius habitat is characterized by dead wood with diameters 20 cm and above. Interpreting this as a limit for dead wood preference places the species with around 60% of saproxylic beetles; while 20% of species prefer diameters exceeding 40 cm (Dahlberg & Stokland 2004). Other studies have shown that saproxylic insect species richness is positively correlated with increasing tree size (Jonsell et al. 1998) and that larger-diameter trees are especially important for red-listed species (Dahlberg & Stokland 2004).

The results for host tree preference support existing knowledge on the wide tolerance of different host tree species (Duffy 1946; Ehnström & Holmer 2007). Only the exclusion of coniferous trees and the unknown category yielded an improvement compared with the full set of tree species, see Fig. 13. Duffy (1946) describes the species as polyfagous with little discrimination between species or between coniferous and deciduous trees, which is noted as unusual for a saproxylic species. Milberg et al (2014) found that a majority out of 171 studied species of saproxylic beetles had low tree-host preferences and Köhler (2000) found that only 13% of species could be said to be tree-host specific at the genus level, so low-host preference, above genus-level, is the norm for saproxylic species. The results of this study suggest that coniferous trees are not suitable as substrate, but since the majority of coniferous trees recorded in the study were in planted production forest, other factors than substrate suitability could influence this, such as spatial organization relative to long-continuity habitat patches. As previously discussed, the catch at Häckeberga Perstorp could be explained by that spruce had acted as substrate, although this is not an overall trend. As previously noted, Scots pine (*Pinus sylvestris*) is a known host tree further up in the country (Ehnström & Holmer 2007), but this species was barely encountered during the surveys. Müller et al. (2015) found that Scots pine was the most common coniferous tree utilized by species that were otherwise broadleaf specialists.

For decomposition stage it is clear that intermediate stages 2-3 are preferred by the beetle, while the late stage 4 is seemingly of little use, see Fig. 12. On a four category scale, decomposition stages 2-3 translated into a time scale give a range of 3-50 years after the death of the tree (Ehnström & Holmer 2007), however the upper limit is likely not applicable except for very dense, slow growth trees that decay very slowly (Dahlberg & Stokland 2004). In their 4-category scale, Jonsell et al. (1998) instead puts stages 2-3 at 2-15 years, which may be a better estimate for the average dead wood object. A general trend seen for saproxylic beetles is that host-specificity decreases from an exclusive set of beetle species that can feed on living trees and cope with the living trees defenses against attack, to an increasing group of species as the tree dies and starts to decay (Müller et al. 2015; Dahlberg & Stokland 2004). As the tree decays, the flora of decomposing fungi becomes the deciding factor for beetle substrate preference and it can be difficult to distinguish saproxylic insects that feed off the wood itself from those that feed on the mycelia of fungi invading the tree (Jonsell et al. 1998). Further research is needed to determine if *P. coriarius* feeds off decayed wood or fungi mycelia and if the species has any associations with certain species of wood-decay fungi.

All types of stumps combined, high stumps, cut stumps and natural stumps are statistically non-significant in relation to catches. It is first when combining the factors decomposition stages and object type that it becomes clear that all three types of stumps together give a significant correlation. The conclusion is reached that the species does not seem to discriminate between taller and low stumps, nor between cut and naturally broken stumps. When the small category of living trees damaged at the base is added, the regression reaches its highest significance level ($p=0.00000306$, $R^2=0.458$). Possibly other types of dead wood can occasionally be utilized as substrate, but not to the extent that they are characteristic for the habitat of the species. Duffy (1946) describes finding developing larvae in a lying log that had been felled after colonization so that the larvae were more or less confined to that substrate.

Hallands Väderö is a key data point, in that when taken out, correlations lose a large amount of explanatory power, see Fig. 16. The question is whether it is problematic to draw conclusions based on correlations so reliant on one data point. Hallands Väderö itself is an excellent locale for saproxylic beetles and has a very high density of dead wood, so there is cause for the site to represent the maximum population in the data set. It can be argued that the population dynamics there could differ from sites on the mainland; the site is an island and the population is therefore confined, which could have contributed to a higher population density than mainland sites would have. However, many of the mainland sites were virtual islands in an agricultural landscape and overall there was significant heterogeneity between sites when it came to factors such as habitat type and land use. Since the species is known from a limited number of sites in Scania, it was not possible to limit the site selection to be more homogenous and is the reason that Hallands Väderö was not omitted from the plots.

THRESHOLD LEVEL

Looking at the final regression plot in Fig. 15f, the line of best fit passes the origin very closely. Had there been an extinction threshold for *P. coriarius*, the line could have been expected to intercept further along the X-axis, as in Fig. 2. The theoretical basis underlying extinction thresholds is related to elevated extinction risks for populations living on little substrate (Ranius & Fahrig). In general, small populations suffer a higher risk of disappearing compared to large populations for demographic reasons as well as environmental and genetic stochasticity (Dempster & Maclean 1998). The absence of an extinction threshold could indicate that *P. coriarius* is not as vulnerable when in small populations compared to other species where extinction thresholds have been detected, and that the species can subsist in small but stable populations on low levels of substrate. There is also the possibility that an existing threshold level was simply not detected. The threshold level could have been obscured due to immigration of individuals from other populations, thereby decreasing the risk of extinction, a phenomenon known as the rescue effect (Brown & Kodrik-Brown 1977). Amongst the study sites, several were grouped together in mosaic areas of suitable habitat, where movement between habitat patches was possible. The method of using pheromone baits could have caused a similar masking of the threshold level by attracting males from other populations in nearby patches. Such possibly confounding factors could be avoided in future studies if the attraction range of the pheromone is determined more precisely and taken into consideration when placing traps.

Although a threshold level was not detected, several populations were small and had little available substrate, see Fig. 15f. These populations are especially vulnerable to gaps on substrate continuity. When only little substrate is available there is an added risk of temporal gaps, where all available dead wood substrate becomes unsuitable before successor trees have died or reached a sufficient decay stage. Such gaps in habitat availability could cause the extinction of small populations, but also of large populations when there is an even age-distribution of host trees and no trees exist to replace them when the substrate has been used up. It is crucial that such gaps are avoided, so that the supply of dead wood resources is secured. This can be done by active management, which may mean that forest managers need to undertake forestry measures more frequently than the normal interval between actions such as thinning or harvesting. Since *P. coriarius* mainly utilizes the roots, the cut tree can still be utilized for timber, which may lower the financial loss for forest owners when implementing conservation measures. Although to benefit other saproxylic species, the dead wood should ideally be left at the site.

FRAGMENTATION EFFECTS?

In this study, several factors suggest that *P. coriarius* has a limited ability to colonize new habitat patches. *P. coriarius* responds to dead wood at a relatively low characteristic scale, 250 m. Holland et al. (2004) have suggested that characteristic spatial scale is thought to be related to the dispersal behavior of a species. The species can utilize cut stumps, which is common substrate in the production forest. As the species has been declining throughout the

past century, this indirectly suggests that the species has a limited dispersal ability not being able to utilize this substrate on a landscape level. It was also noted that several unoccupied sites with suitable substrate occurred in relatively close proximity to occupied sites, suggesting fragmentation effects. This is highlighted well by the site Hjällen, a site with a very high density of beech deadwood where *P. coriarius* is absent. This site is located at a distance of 4 km from two sites where the species was caught. Other examples of such sites were Haväng, Bellinga Pasture and Sövdesjön Ranås (where the one caught male had likely flown from another site). These suggestions of dispersal-limitation are supported by the results of an unpublished study on *P. coriarius* in Söderåsen National Park (Mattias C. Larsson, personal communication). Individuals were only caught in, and in close proximity to, the Skäralid ravine, an area of longer forest continuity compared to the surrounding beech forest, which could suggest that the species is very slow when colonizing new habitat, although in that specific area the local topography could have contributed to the slow colonization process.

The female *P. coriarius* is responsible for colonizing new habitat when ovipositing on dead wood substrate, so the limited dispersal should be explained by the behavior or flight capacity of the female. Because the female produces the sex pheromone, she can simply wait for males to arrive and therefore may have less to gain by moving away from the home patch, promoting a tendency to stay there. Since the male needs to search for a female, he could benefit more by increased mobility. Certain sites studied, with only a single caught male suggests fly-in males and gives some indication that males are capable of leaving their home patch. Duffy (1946) writes that the species, especially the males, can sometimes conduct long-scale flight. Sex-based differences in physiological dispersal capacity have been observed in *Osmoderma eremita*, a species in which the male produces the pheromone (Larsson et al. 2003). In lab experiments, female *O. eremita* had better physiological dispersal capacity compared to males (Dubois et al. 2010). The behavioural inclination to disperse measured in the field is low however and here no difference has been found between sexes, although the number of individuals included in the study was limited (Ranius & Hedin 2001).

Since 1996, the amount of dead wood in Swedish forests has been increasing (Skogsstyrelsen 2014). This can partly be attributed to the development of new forestry practices in the past 20 years, including certification schemes, which require that some dead wood as well as living trees are left at clear cuts for conservation purposes (Roberge et al. 2015). There is a risk that retained dead wood on a landscape level becomes too spread out and therefore ineffective in benefiting *P. coriarius* and other dispersal limited beetles. Forest managers should be advised that larger, collected areas with spatially connected dead wood resources are favourable compared to small scattered stands in the landscape. Situating dead wood resources in a cluster with radius not exceeding 250 m would ensure that the species does not experience fragmentation effects. Brunet and Isacsson (2009) also proposed that new dead wood resources should be situated close to existing populations for red-listed beetles dependent on beech high stumps. Johansson et al. (2013) suggested that it will benefit many species to assemble retained deadwood resources in select places so that high levels of deadwood can be maintained in a few locations rather than having a low but even level of dead wood overall.

Clear cuts as habitat

Cut stumps have been shown in this study to be useful to *P. coriarius* as habitat and there were indications from the site Maglehems Ora that clear cuts can on occasion sustain large *P. coriarius* populations, at least for a short time period. On a clear cut, all dead wood substrate is created at the time of harvest without the possibility of recruitment of new suitable dead wood resources when the cut stumps become too decayed. Furthermore, assuming that the species has poor dispersal ability, few clear cuts will be colonized where *P. coriarius* was not already present. The utility of clear cuts must therefore be regarded as

limited and in many cases clear cuts will have a directly negative effect on local populations. It is possible that the humid and dark conditions imposed as a new forest grows at a clear cut may speed up the degradation process of the dead wood object. It may also be so that the dark and impassable conditions in the undergrowth could make copulation and oviposition more difficult. For species dependent on sun-exposed deadwood, such as *Tragosoma depsarium,* undergrowth on clear cuts will shade out deadwood logs and lead to a reduction in the substrate's persistence period (Wikars 2003). There is still much to discover about how clear cuts compare to natural forest as *P. coriarius* habitat, and if it is possible to maintain viable populations of *P. coriarius* in production forests that are clear cut harvested.

Further studies

More research is needed to gain a complete understanding of the substrate requirements of *P. coriarius*. There are several additional factors that could be important when characterizing *P. coriarius* habitat, such as substrate humidity and soil type. Different sources highlight somewhat of a dichotomy on the needed humidity of the dead tree substrate. Duffy (1946) suggested that the species is dependent on sufficient humidity level in the ground while Ehnström and Holmer (2007) describe the optimum habitat instead as a dry and sandy pine forest and that the microclimate in a closed, production forest has been described as negative to the species (Ljungberg & Ehnström 2016). Soil type is another factor that could be important, seeing as the species uses soil particles to form its cocoon (Ehnström & Holmer 2007).

More knowledge is needed on the dispersal of the species and to what extent it is impacted by habitat fragmentation. Such studies should be focused on the dispersal behavior of the females. To accomplish this, other methods than the pheromone trapping used in this study are needed, since the substance only attracts males. A mark-release-recapture scheme involving female *P. coriarius* could give indications on their dispersal abilities. Another suggestion is to use radio tracking, by finding a female beetle, tagging it with small radio transmitter and then monitoring the animal and recording its movements. Both these suggestions must overcome the difficulty of detecting and recapturing the females, which are typically elusive and mostly nocturnal. Alternatively, a study on genetic variation between and within populations could make use of pheromone trapping and provide indirect information on dispersal by how genetically distinct different populations are.

Developing a better understanding of the time scales of colonization and substrate utilization at clear cuts is important for informing deciduous forestry management suitable for *P. coriarius*. The population dynamics at clear cuts could be highly fluctuating with populations spikes occurring 5-15 years after a clear cut is formed and the stumps develop into usable substrate, followed by a marked decline as stumps become too degraded. Using pheromone traps, clear cut population dynamics can be studied over several years starting when a clear cut is first established, alternatively as a space-for-time study using different comparable clear cut sites of different ages.

Implications for conservation

The results of this study could suggest that a decrease of substrate availability is not the main explanation for the negative development of *P. coriarius*; the species is able to utilize cut stumps on clear cuts, which are ubiquitous in the Swedish forest landscape. It is proposed that other factors are preventing the species from exploiting these substrate resources, most likely dispersal limitation. It is unlikely that populations can be maintained in habitat that is clear cut harvested, as substrate continuity is not maintained. A possible solution is to leave retention trees on clear cuts to provide dead wood after the substrate provided by cut stumps is no longer suitable. Where the species is present, it would be preferential if forest owners go together and group dead wood and retention trees instead of scattering them over large distances. Selection cutting could be a beneficial alternative for *P.*

coriarius compared to clear cutting, giving a more stable supply of dead wood in the form of cut stumps (Skogsstyrelsen 2011). In existing populations, more dead wood resources should be primarily focused close to inhabited patches, especially where populations are small. Given the existence of sites such as Hjällen, with high levels of suitable substrate but seemingly out of the dispersal range of nearby *P. coriarius* populations, it makes sense to investigate the possibility of assisted colonization as a measure to establish new populations that based on substrate availability could develop into some of the largest populations of *P. coriarius* in Scania.

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REFERENCE LIST

Barbour JD, Millar JG, Rodstein J, Ray AM, Alston DG, Rejzek M, Dutcher JD, Hanks LM (2011) Synthetic 3,5-Dimethyldodecanoic Acid Serves as a General Attractant for Multiple Species of Prionus (Coleoptera: Cerambycidae). Annals of the Entomological Society of America 104: 588-593.

Bergman K-O, Jansson N, Claesson K, Palmer MW, Milberg P (2011) How much and at what scale? Multiscale analyses as decision support for conservation of saproxylic oak beetles. Forest Ecology and Management 254: 133-141.

Brown JH, Kodrik-Brown A (1977) Turnover Rates in Insular Biogeography: Effect of Immigration on Extinction. Ecology 58: 445-449.

Brunet J, Isacsson G (2009) Restoration of beech forest for saproxylic beetles—Effects of habitat fragmentation and substrate density on species diversity and distribution. *Biodiversity and Conservation*, 18: 2387–2404.

Dahlberg A, Stokland JN (2004) Vedlevande arters krav på substrat (Rapport No. 7). Jönköping: Skogsstyrelsen.

Dempster JP, McLean IFG (eds.) (1998) Insect populations - in theory and practice. Springer Science + Business Media, Dordrecht.

Dubois GF, Le Gouar PJ, Delettre YR, Brustel H, Vernon P (2010) Sex-biased and body condition dependent dispersal capacity in the endangered saproxylic beetle *Osmoderma eremita* (Coleoptera: Cetoniidae). Journal of Insect Conservation 14: 679-687.

Duffy E (1946) A contribution towards the biology of *Prionus coriarius* l. (Coleoptera, Cerambycidae). Transactions of the Royal Entomological Society of London 97: 419-442.

Ehnström B, Axelsson R (2002) Insektsgnag i bark och ved. ArtDatabanken, Uppsala.

Ehnström B, Holmer M (2007) Nationalnyckeln till Sveriges flora och fauna. Skalbaggar: Långhorningar. Artdatabanken. Uppsala.

Franc N, Götmark F, Økland B, Nordén B, Paltto H (2007) Factors and scales potentially important for saproxylic beetles in temperate mixed oak forest. Biological Conservation 135: 86–98.

Gibb H, Hjältén J, Ball JP, Atlegrim O, Pettersson RB, Hilszczanski J, Johansson T, Danell, K (2006) Effects of landscape composition and substrate availability on saproxylic beetles in boreal forests: a study using experimental logs for monitoring assemblages. Ecography 29:191–204.

Gärdenfors U (ed) (2015) Rödlistade arter i Sverige 2015. ArtDatabanken, Uppsala.

Hanski I, Pakkala T, Kuussaari M, Lei G (1995) Metapopulation persistence of an endangered butterfly in a fragmented landscape. Oikos 72:21–28

Holland JD, Bert DG, Fahrig L (2004) Determining the spatial scale of species' response to habitat. BioScience 54: 227-233.

Johansson T, Hjältén J, de Jong J, von Stedingk H (2013) Environmental considerations from legislation and certification in managed forest stands: A review of their importance for biodiversity. Forest Ecology and Management 303: 98-112.

Jonsell M, Weslien J, Ehnström B (1998) Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodiversity and Conservation 7: 749–64.

Köhler F (2000) Totholzkäfer in Naturwaldzellen des nördlichen Rheinlandes. Vergleichende Studien zur Totholzkaferfauna Deutschlands und deutschen Naturwaldforschung Recklinghausen: Landesamt Agrarordnung NRW.

Larsson MC, Hedin J, Svensson GP, Tolasch T, Francke W (2003) Characteristic odor of Osmoderma eremita identified as a male-released pheromone. Journal of Chemical Ecology 29: 575–587.

Larsson MC, Svensson GP (2011) Monitoring spatiotemporal variation in abundance and dispersal by a pheromone-kairomone system in the threatened saproxylic beetles *Osmoderma eremita* and *Elater ferrugineus*. Journal of Insect Conservation 15: 891-902.

Lindhe A, Jeppson T, Ehnström B (2010) Longhorn beetles in Sweden – changes in distribution and abundance over the last two hundred years. Entomologisk tidskrift 131.

Ljungberg H, Ehnström B (2016) Artfaktablad Taggbock *Prionus coriarius*. Artdatabanken, SLU. Available at: http://artfakta.artdatabanken.se/taxon/101629 (2016-02-24).

Milberg P, Bergman K-O, Johansson H, Jansson N (2014) Low host-tree preferences among saproxylic beetles: a comparison of four deciduous species. Insect Conservation and Diversity 7: 508-522.

Müller J, Butler R (2010) A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. European Journal of Forest Research 129: 981-992.

Müller J, Wende B, Strobl C, Eugster M, Gallenberger I, Floren A, Steffan-Dewenter I, Linsenmair KE, Weissner WW, Gossner MM (2015) Forest management and regional tree composition drive the host preference of saproxylic beetle communities. Journal of Applied Ecology 52:753-762.

Nilsson SG, Baranowski R (1997) Habitat predictability and the occurrence of wood beetles in old-growth beech forests. Ecography 20: 491-498.

Økland B, Bakke A, Hågvar S, Kvamme T (1996) What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. Biodiversity and Conservation 5: 75-100.

Paletto A, De Meo I, Cantiani P, Ferretti F (2013) Effects of forest management on the amount of deadwood in Mediterranean oak ecosystems. Annals of Forest Science 71: 791-800.

Ranius T, Hedin J (2001) The dispersal rate of a beetle, *Osmoderma eremita*, living in tree hollows. Oecologia 126: 363–370.

Ranius T (2002) Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. Biological Conservation, 103: 85-91.

Ranius T, Fahrig L (2006) Targets for maintenance of dead wood for biodiversity conservation based on extinction thresholds. Scandinavian Journal of Forest Research 21: 201-208.

Roberge J-M, Lämås T, Lundmark T, Ranius T, Felton A, Nordin A (2015) Relative contributions of set-asides and tree retention to the long-term availability of key forest biodiversity structures at the landscape scale. Journal of Environmental Management 154: 284-292.

Rodstein J, McElfresh JS, Barbour JD, Ray AM, Hanks LM, Millar JG (2009) Identification and Synthesis of a Female-Produced Sex Pheromone for the Cerambycid Beetle Prionus californicus. Journal of Chemical Ecology 35: 590-600.

Schiegg K (2000) Effects of dead wood volume and connectivity on saproxylic insect species diversity. Ecoscience 7: 290–298.

Skogsstyrelsen (2014) Skogsstatistisk årsbok 2011. Skogsstyrelsen, Jönköping.

Skogsstyrelsen (2011) Kontinuitetsskogar och hyggesfritt skogsbruk – Slutrapport för delprojekt naturvärden. Available at: http://www.skogsstyrelsen.se/Global/myndigheten/Projekt/kontinuitetsskog%20och%20hyggesfritt/Rapport_7_2011_Kontinuitetsskogar%20och%20hyggesfritt%20skogsbruk_Slutrapport%20f%C3%B6r%20delprojekt%20naturv%C3%A4rden.pdf (2016-02-23).

Wikars L-O (2003) Raggbocken (Tragosoma depsarium) gynnas tillfälligt av hyggen men behöver gammelskogen. Entomologisk Tidskrift 124: 1-12.

APPENDIX

Table 3: Total catches, mean catches, descriptive statistics of catches and centroid coordinates in RT90

Site name	Total catch	Mean catch	Standard Deviation	Coefficient of variation	Centroid, X	Centroid, Y	Surveyed?
Nällåkraskogen	1	0.333	0.577	1.73	6226818	1304031	No
Sövdesjön Ranås	1	0.333	0.577	1.73	6163099	1365179	No
St Olof	1	0.333	0.577	1.73	6168144	1394190	No
Fulltofta East	2	0.667	0.577	0.87	6196551	1365078	No
Fyledalen Röddinge	4	1.33	0.577	0.43	5151887	1376477	Yes
Mölleröds kungsgård	4	1.33	0.577	0.43	6228184	1369850	Yes
Rävstad	5	1.67	2.08	1.25	6160658	1344413	Yes
Herrevadskloster North	6	2.00	1.00	0.50	6222971	1341412	Yes
Frualid	7	2.33	2.08	0.89	6175140	1366060	Yes
Bellinga West Forest	7	2.33	4.04	1.73	6157353	1366276	Yes
Dunderbäcken	8	2.67	3.06	1.15	6187310	1395244	Yes
Torsebro	9	3.00	1.73	0.58	6221052	1395289	Yes
Vitabäckshällorna	10	3.33	4.93	1.48	6163921	1372765	Yes
Froenahejdan	11	3.67	3.21	0.88	6171337	1382357	Yes
Fyledalen Skogshejdan	20	6.67	1.15	0.17	6160129	1375172	Yes
Söderåsen East	20	6.67	1.15	0.17	6214250	1341161	Yes
Söderåsen West	20	6.67	1.53	0.23	6163098	1366132	Yes
Kvesarum	25	8.33	6.66	0.80	6204915	1365137	Yes
Fyledalen Nyvångsskogen	29	9.67	5.86	0.61	6161088	1375925	Yes
Snogeholm	30	10.0	5.29	0.53	6161305	1367894	Yes
Svaneholm*	22	11.0	7.07	0.64	6155180	1352576	Yes
Sövdeborg West	33	11.0	3.46	0.31	6163098	1366132	Yes
Stenshuvud	36	12.0	5.57	0.46	6170637	1402957	Yes
Fulltofta West	37	12.3	5.13	0.42	6196683	1361813	No
Dörröds fälad	40	13.3	4.04	0.30	6165546	1352135	Yes
Söderåsen North	53	17.7	7.64	0.43	6215447	1339765	Yes
Klintabäcken	59	19.7	11.7	0.60	6200140	1384433	Yes
Näsums bokskog	60	20.0	16.6	0.83	6228362	1420420	Yes
Herrevadskloster South	63	21.0	10.4	0.50	6220872	1340651	Yes
Torup 2	76	25.3	8.14	0.32	6161777	1335906	Yes
Christinehof Ecopark	76	25.3	15.3	0.60	6178538	1383820	Yes
Torup 1	80	26.7	5.13	0.19	6161424	1336994	No
Åbjär	81	27.0	21.4	0.79	6195353	1387184	Yes

Torup 3	82	27.3	15.9	0.58	6160699	1336329	Yes
Ekhagsvägen	83	27.7	7.51	0.27	6159019	1339532	Yes
Häckeberga Husarahagen	89	29.7	12.7	0.43	6160563	1349409	Yes
Häckeberga Swamp	89	29.7	14.4	0.48	6162578	1349371	No
Eksholm	91	30.3	20.5	0.68	6161378	1342542	Yes
Häckeberga Skoggård	96	32.0	17.1	0.53	6163422	1348763	Yes
Julebodabäcken	103	34.3	14.0	0.41	6182974	1396791	Yes
Forsakar	113	37.7	26.8	0.71	6189961	1391433	No
Sövdeborg East	118	39.3	8.50	0.22	6163128	1367252	Yes
Vrams Gunnarstorp	133	44.3	7.77	0.18	6223540	1323883	No
Ravlunda West	203	67.7	1.53	0.02	6181410	1395588	Yes
Ravlunda skjutfält*	140	70.0	15.6	0.22	6180408	1397069	Yes
Häckeberga Perstorp*	155	77.5	88.4	1.14	6163757	1352649	Yes
Vegeholm	265	88.3	27.2	0.31	6234848	1314094	No
Maglehems Ora	365	122	28.0	0.23	6181129	1394883	Yes
Hallands Väderö	605	202	62.8	0.31	6261563	1300279	Yes
Hjällen	0	0	0	-	6200759	1365939	Yes
Tvedöra	0	0	0	-	6176435	1349985	Yes
Prästaskogen	0	0	0	-	6175639	1349120	No
Börringekloster Woodland	0	0	0	-	6155871	1341903	Yes
Börringekloster Grassland	0	0	0	-	6156142	1343514	Yes
Haväng	0	0	0	-	6178571	1398722	Yes
Klammersbäcken	0	0	0	-	6176902	1398748	No
Bellinga Pasture	0	0	0	-	6157017	1368650	No

*One trap had fallen down, two traps used for analysis.